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Notes on the genus *Ahexaroptrum* with a description of new species (Coleoptera: Tenebrionidae: Coelometopinae)

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Abstract. A second species of the genus *Ahexaroptrum* Kaszab, 1960, *A. schawalleri* sp. n. is described from the Cameron Highlands in West Malaysia and compared to *A. humeridens* Kaszab, 1960. Male genitalia and habitus of both species are illustrated and a key to the species of *Ahexaroptrum* is given.

Taxonomy, new species, bionomy, key, Coleoptera, Tenebrionidae, Coelometopinae, *Ahexaroptrum*, Oriental region

INTRODUCTION

The description of the monotypic genus *Ahexaroptrum* Kaszab, 1960 was based on two specimens of *A. humeridens* collected in West Malaysia. Since Kaszab's description no information about this taxon has been published. The author collected the genus on one of two known localities in January and June 1995. Adult beetles were found on a several-year-old clearing close to the base of the Jasar mountain in the Cameron Highlands. The material contains *A. humeridens* and one new species which is described below.

MATERIAL AND METHODS

All measurements used for the description of the new species were made on the holotype. The variability of measured characters was not significant if not mentioned otherwise. Total length of a species is distance from the clypeus up to elytral apex when the head is in natural bent position. The position of a tooth on the inner margin of meso- and metafemur is given in respect to maximal length of the femur. Square brackets used in the text indicate author's remarks.

Specimens of the newly described species are always provided with one printed red label: „Holotype (or Paratype) *Ahexaroptrum schawalleri* sp. nov. [handwritten] S. Bečvář det. 1997 (or 1996)". All material studied is deposited in the following collections (the number of specimens examined is found in the abbreviated form, e. g. 1 HBCH means 1 specimens in the Collection of H. J. Bremer, Heidelberg, Germany):

HNHM – Hungarian Natural History Museum, Budapest, Hungary (O. Merkl)
HBCH – Collection H. J. Bremer, Heidelberg, Germany
JFCH – Collection J. Ferrer, Haninge, Sweden
KMCY – Collection K. Masumoto, Yokohama, Japan
MLCS – Collection M. Lillig, Saarbrücken, Germany
MNHN – Muséum National d'Histoire naturelle, Paris, France (C. Girard)
NMPC – National Museum Prague, Czech Republic (J. Jelínek)
SBCB – Collection S. Bečvář, České Budějovice, Czech Republic
SMNS – Staatliches Museum für Naturkunde, Stuttgart, Germany (W. Schawaller)
RGCT – Collection R. Grimm, Tübingen, Germany

SYSTEMATIC PART

Ahexaroptrum Kaszab, 1960

Ahexaroptrum Kaszab, 1960: 291.

TYPE SPECIES. *Ahexarhoptrum humeridens* Kaszab, 1960: 292 (by monotypy).

DIAGNOSIS. Body elongate, (length 16.5–19.7, width 6.7–8.2), strongly convex; colouration piceous. Pronotum subhemispheric, nearly as long as wide, smooth.

Elytra with conspicuous humeral tooth; elytral base flattened, elytral disc strongly convex, posteriorly with more or less developed interstrial swellings. Legs long. Femora claviform. Aedeagus strongly flattened in dorso-lateral view. Parameres broad, with widely separated apices. Each paramere with an acute, median, dorsal projection (forming a „pouch" for the apex of penis). Penis with base enlarged, drop-shaped in ventral view; apex very slender, pointed.

BIONOMY AND DISTRIBUTION. Both known species are crepuscular and nocturnal tenebrionids living on the trees in forested highlands of West Malaysia. Larvae are unknown but very probably live in rotting wood. Adults probably do not fly. Two examined specimens were found to be slightly brachypterous, with metathoracic wings about as long as elytra.

TAXONOMY. The shape of the aedeagus suggests that the genus *Ahexaroptrum* stands in a rather isolated position among other related genera. Only some species of the genus *Derosphaerus* Thomson, 1858 have a similar shape of aedeagus (see figs 95–100 in Kaszab 1987).

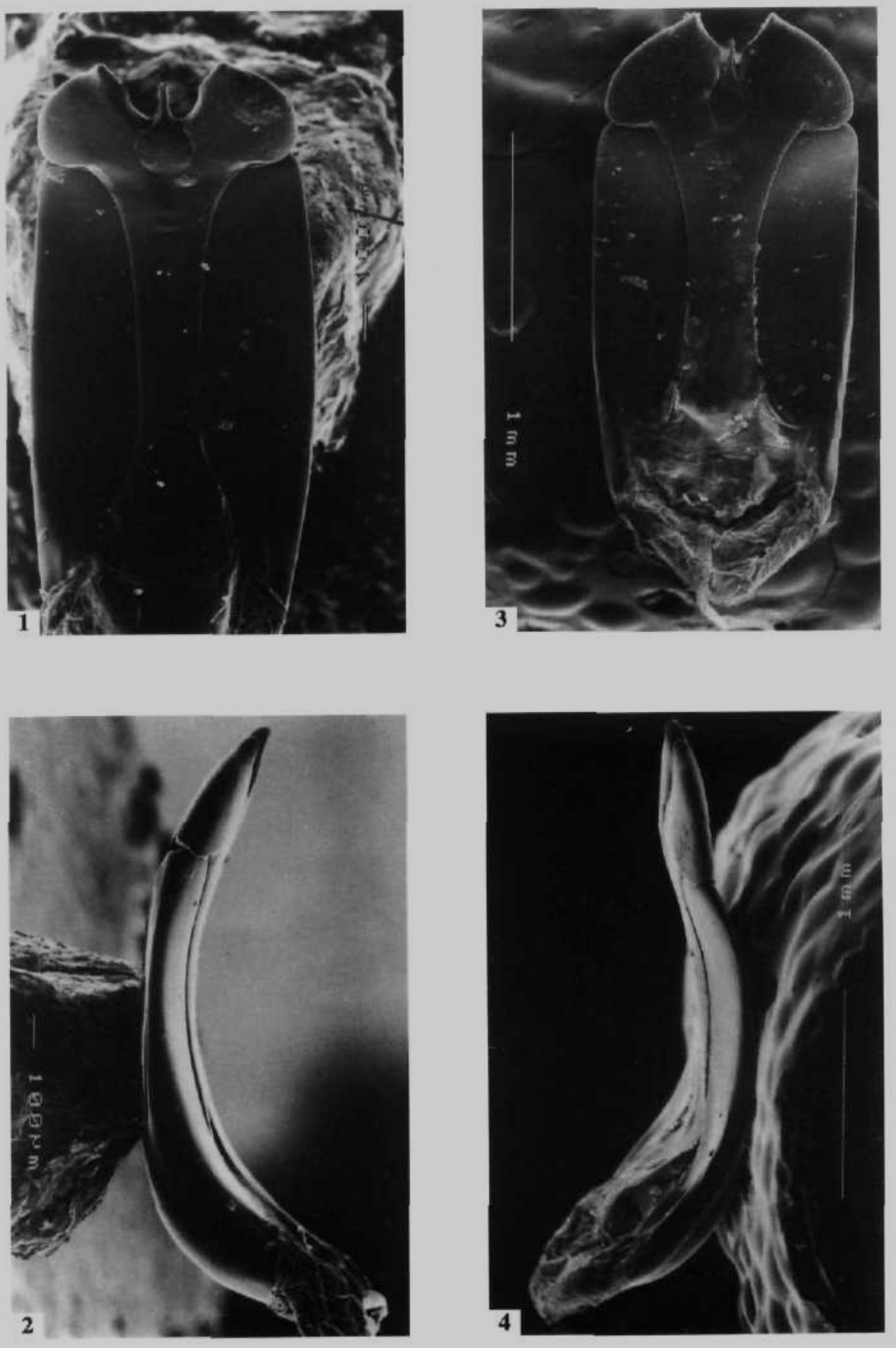
Kaszab (1964) placed *Ahexaroptrum* close to the genus *Hexarhopalus* Fairmaire, 1891 without giving any explanation. However, at least two other genera, *Derosphaerus* and *Asbolodes* Fairmaire, 1893 should be taken into consideration when evaluating the phylogenetical status of *Ahexaroptrum*.

The present paper retains *Ahexaroptrum* in the tribe Coelometopini of the subfamily Coelometopinae. This placement is in accordance with the conclusions of Doyen & Tschinkel (1982), who on the basis of phylogenetic analysis placed the genera *Derosphaerus*, *Misolampidius*, and *Necrobioides* in the Coelometopini and coelometopine lineage. All the genera mentioned above and many others appear to represent a rich group of probably monophyletic clades of Coelometopinae genera. The important synapomorphic character of this diverse group seems to be the claviform femora. A thorough phylogenetical analysis of the enormously diverse subfamily Coelometopinae is highly needed.

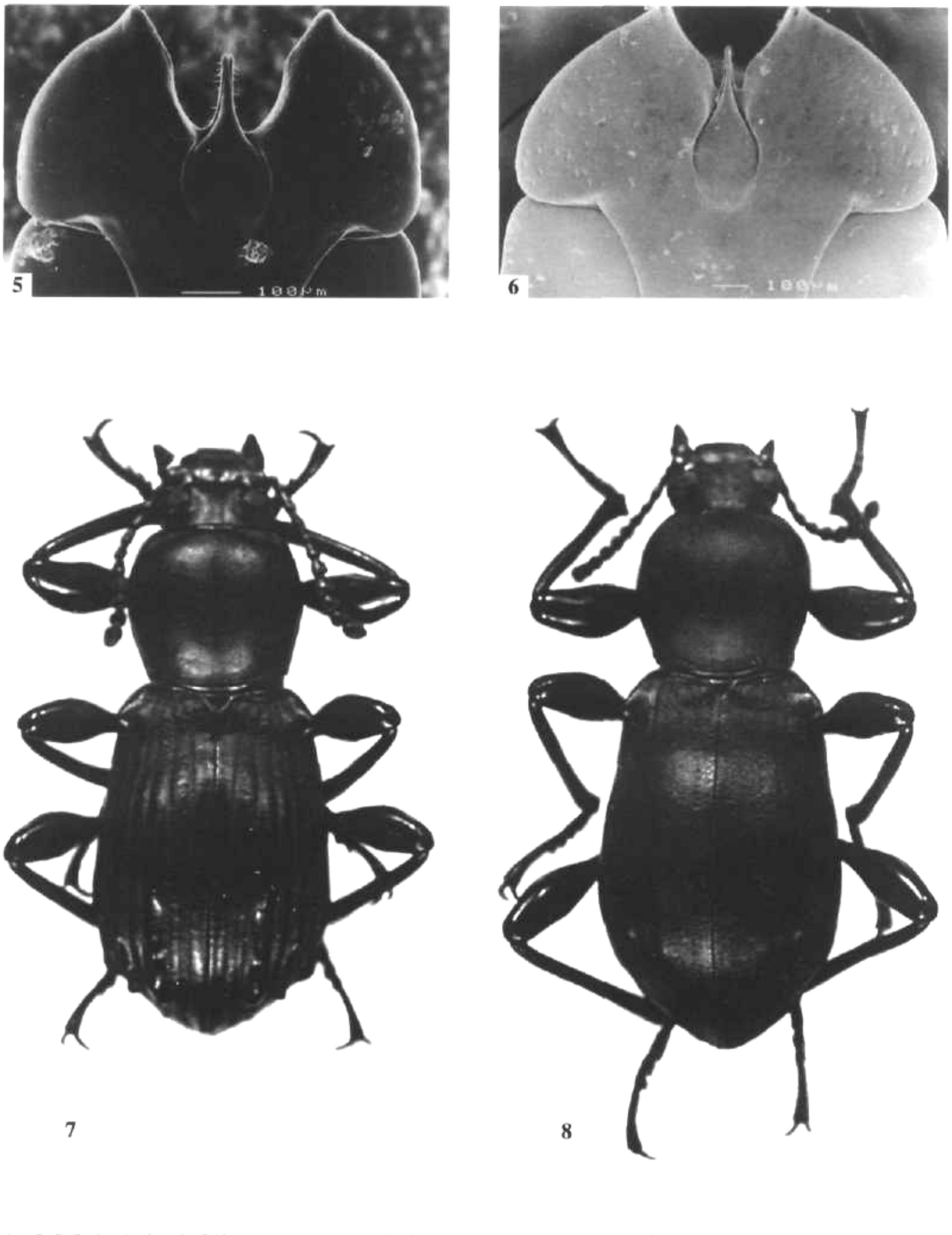
Key to the species of *Ahexaroptrum*

1(2) Elytral interstriae convex posteriorly. Interstria 3, 5, 7 and 9 more distinctly convex, with several obvious tubercles and longitudinal swellings in posterior half (Fig. 7). Males without a tooth on the inner margin of meso- and metafemur. Apex of male protibia on the inner margin only slightly dilated. Aedeagus as in Figs 1, 2 and 5. Parameres moderately wide, their maximal combined width 4.6 times as large as maximum width of penis. Both emarginations between mesal margin of parameres and median projection combined broader than penis. .... *A. humeridens* Kaszab.

2(1) Elytral interstriae flat. Interstria 3, 5, 7 and 9 only with several reduced and fine swellings in posterior half (Fig. 8). Males with a tooth on the inner margin of meso- and metafemur at basal 0.25–0.3. Apex of male protibia on the inner margin dilated and tooth-shaped. Aedeagus as in Figs 3, 4, and 6. Parameres very wide, their maximal combined width 6.5 times as large as maximum width of penis. Both emarginations between mesal margin of parameres and median projection combined obviously narrower than penis. .... *A. schawalleri* sp. n.



Figs 1–4. Aedeagi of *Ahexaroptrum* spp. (1–3 ventral view, 2–4 lateral view). 1–2 *A. humeridens* Kaszab. 3–4 *A. schawalleri* sp. n.



Figs 5–8. 5–6 – Aedeagi of *Ahexaroptrum* spp. (apical portion of parameres – ventral view). 5 – *A. humeridens* Kaszab. 6 – *A. schawalleri* sp. n. 7–8 – Body shape of *Ahexaroptrum* spp. 7 – *A. humeridens* Kaszab (male, length 17.3 mm). 8 – *A. schawalleri* sp. n. (holotype, length 17.7 mm).

Ahexarhoptrum humeridens Kaszab, 1960
(Figs 1, 2, 5, 7)

Ahexarhoptrum humeridens Kaszab, 1960: 292 (by monotypy).

TYPE MATERIAL. The holotype (not examined) is deposited in The Natural History Museum, London, United Kingdom: [West Malaysia], Perak, Taiping; Paratype (examined). 1 HNHM: [West Malaysia], Pahang, Cameron's Highland, Rhododendron Hill, 5200 ft, 13. x. 1923.
ADDITIONAL MATERIAL. 1 male SBCB: West Malaysia, Pahang, C. Highlands, Tanah Rata, 20.–25.1.1995 Gn. Jasar, 14–1500 m, lgt. S. Bečvář j. & s.; 1 male KMCY: Malaya [West Malaysia], Cameron Highlands, 26.4.1993, H. Karube leg.; 1 female JFCH: Malaysia, Cameron Highland, 16.iii.1981, rec. K. A. Pehrson.

DISTRIBUTION. West Malaysia.
DIFFERENTIAL DIAGNOSIS. See the key for the separation from *A. schawalleri* sp. n.

Ahexarhoptrum schawalleri sp. n.
(Figs 3, 4, 6, 8)

HOLOTYPE. Male NMPC: West Malaysia, Pahang, C. Highlands, Tanah Rata, 20.–25.1.1995 Gn. Jasar, 14–1500m, lgt. S. Bečvář j. & s.
PARATYPES. 1 male and 2 females SBCB, 1 male HBCH, 1 male KMCY, 1 male MLCS: same data as holotype; 4 males and 3 females SBCB, 1 male RGCT: 19.–25.6.1995, lgt. S. Bečvář, other data as the holotype; 1 SMNS: [West] Malaysia, Cameron Highlands, Gn. Brinchang, 20.iv.1990 leg. A. Riedel; 2 males, 3 females JFCH: Malaysia, Pahang, February 1994, Kampong Raya, lgt. Jörgen Nielsen; 1 HNHM: Malaysia, Pahang, Cameron Highlands, Tana Rata, Gunung Beremban, mountain rain forest, from beneath bark & from bracket fungi, 1700 m, 28.iii.1995, # 92, [lgt.] O. Merkl; 1 female MNHN: W-Malaysia, Cameron Highlands 3.x.1973, C. C. Chua leg.; 1 female MNHN: W-Malaysia, Cameron Highlands, 9.ii.1974, C. C. Chua leg.

DESCRIPTION. Body elongate and strongly convex, colouration piceous, integument slightly shiny, microshagreened, glabrous and smooth. Legs with developed sexual dimorphism.

Head widest in level of eyes, narrower than pronotum in ratio 0.68, minutely punctured, dorsally flattened. Fronto-clypeal sulcus widely U-shaped, reaching clypeal margin, its base impressed. Anterior margin of clypeus straight. Genae robust, rounded, moderately upturned. Eyes moderately large, vertically reniform, anterior margin moderately concave. Ocular sulci not developed. Antenna 1.05 times as long as pronotum.

Pronotum convex, subhemispheric, broadest at midlength, nearly as long as wide; pronotal margin moderately fully rimmed; basal rim strong, shortly continuing on smooth, not punctured hypomeron. Disc smooth with minute punctation.

Elytra obovate, 1.64 times as long as wide, 2.4 times as long as and 1.41 times as wide as pronotum, highest at midlength, broadest in ca. posterior 0.3. Disc in basal ca. 0.1 flattened, then regularly and strongly convex. Interstriae flat and microwrinkled, only first interstria slightly convex posteriorly; interstria 7 with a prominent, basal tooth; interstria 3, 5, 7 and 9 with several fine swellings in posterior half of elytra. Elytral striae fine, not impressed, strial punctures very fine and sparse.

Prosternum and hypomeron nearly smooth; prosternal process with shallow median groove, rugose apically. Mesosternum rugose with sparse hairs and with short median carina in anterior portion, smooth posteriorly. Metasternum rugose on anterior process, smooth posteriorly. Abdominal ventrites finely longitudinally wrinkled and/or finely punctured.

Legs robust, relatively long. Femora claviform, obviously thickened towards apex. Inner margin of meso- and metafemur with a blunt tooth at basal 0.25–0.3. Tibiae straight, very slightly thickening apicad; outer margin of protibia slightly flattened and concave in apical 0.3; inner margin of male protibia more dilated and tooth-shaped apically.

Aedeagus (Figs 4, 5 and 6) strongly flattened dorso-ventrally; apices of parameres widely separated; parameres very broad, their maximal combined width 6.5 times as large as maximum width of penis; both emarginations between mesal margin of parameres and median projection combined obviously narrower than penis.

FEMALE. Inner margin of protibia without apical tooth. Inner margin of middle and posterior femora simple, without a tooth. Ovipositor feebly sclerotised, simple, slender; apex with long and sparse setae.

LENGTH. 17–19.7 mm (holotype 17.7 mm), width: 6.7–8 mm (holotype 7 mm).

DISTRIBUTION. West Malaysia.

DIFFERENTIAL DIAGNOSIS. See the key for the separation from *A. humeridens*.

NAME DERIVATION. I take a great pleasure in naming this species in honor of Wolfgang Schawaller (Stuttgart), a renowned Tenebrionidae specialist.

Acknowledgements

Thanks are due to the staff of The Laboratory of Electron Microscopy (Institute of Parasitology, České Budějovice) for the help with preparing the SCAN microphotographs. I am also very grateful to my colleagues David Boukal (České Budějovice) and David Král (Praha) who critically commented the manuscript. For practical help with Figs 7 and 8, I am obliged to my colleagues Petr Švácha and Michal Žurovec (České Budějovice).

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PTPT, the freeware program for permutation testing concordance between phylogeny and the distribution of phenetic traits

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Abstract. An idispensable step of any comparative study is the testing of a concordance between distribution of phenetic traits and evolutionary history of the taxon under study. We present a computer program PTPT which can perform these testing on the basis of a permutation tail probability test. The program that can also perform the permutation tests analogical to t-test, analysis of variance (ANOVA) and to correlation analysis is available at http://www.karlin.mff.cuni.cz/~zaboj/ptpt.

Permutation test, phylogeny, phylogenetic tree, program, parasite, *Toxoplasma*, *Trichomonas*

The testing of concordance between the distribution of a particular trait and the evolutionary history of a taxon is a principal task of all comparative studies. The distribution of a trait within the taxon can reflect either distribution of a common function and therefore of a common selective pressure pattern (the species subjected to the same selective pressure have the same trait) or the evolutionary history of the taxon (the phylogenetically relative species share the traits) (Harvey & Pagel 1991). The existence of statistically significant association between the distribution of the trait and the position of the taxon within the genealogical tree indicates the validity of a null hypothesis, i. e., the distribution of the trait simply reflects a random process – the evolutionary history of the taxon cladogenesis (Archie 1989).

Several approaches are being used for testing this null hypothesis depending on the type of data (character set/distance matrices) of the studied trait. If the trait is described by character data, a cladistic analysis can be performed with forced tree topology (reflecting the already known cladogenesis of the taxon). The consistency index provided by common cladistic programs can be used as simple measure of the degree of concordance between distribution of the trait and the phylogeny. The null model can be tested by a permutation tail probability test (Moore et al. 1994). If the trait is described by distance data, Mantel tests can be used to test one or more hypotheses (independent variables represented as matrices) against an observed pattern (dependent matrix) using (partial) regression or correlation (Thorpe 1996).

The later method is more universal because any character data can be transformed to distance matrices. However, before analysis the distances should be corrected for differences in rates of evolution in different branches of phylogram. Moreover, no integrated software is available neither for Mantel test nor for other important types permutation tests.

Recently we developed program PTPT for various types of permutation tail probability tests, including those for analysis of concordance between distribution of traits and phylogeny. The program can analyze the qualitative and quantitative character data as well as the distance matrices. The phylogenetic tree can be entered in usual parenthetical format. The average distance between sister OTUs (operational taxonomic units, i. e., sister strains or sister branches of the tree) is calculated (or read from a distance matrix) and used as a measure of concordance which is tested in one-sided or two-sided permutation tail test (Manly 1991). The program can either generate all possible permutations of terminal branches of the tree or the number of trees to be generated can be user-defined. Usually 5000 random trees provide stable estimation of p-value and can be generated by ordinary PC within seconds.

EXAMPLES

Example 1 – Concordance between the pathogenicity and genealogical relationship of *Trichomonas vaginalis* strains

Pathogenic effects of ten *T. vaginalis* strains on donor female patients were assessed by clinical and histopathological findings and rated by five arbitrary units (0 – no effect, 4 – the most severe effects) (Kulda 1989) (page 148). The phylogenetic (genealogical) tree of trichomonad strains obtained from DNA-fingerprinting data by Neighbor Joining method was ((((((((Tv79–49 Tv10–02) Tv73–87) Tv67–77) Tv7–37) Tv14–85) Tv 85–08) Tv71–96) (FF28 JH–31A)) and the pathogenicity indexes were 1, 1, 2, 2, 4, 4, 2, 2, 0 and 0, respectively (Fig. 1). The concordance between position of the strain within the tree and the pathogenicity indexes was estimated by a permutation test.

At first we can run the PTPT program with the option –h to receive a help screen:

input:

```
>ptpt   –h
```

output:

```
usage PTPT [option] [file]

–h       help
–v       verbose, print partial results
–V       Verbose, print permutations too
–s       suppress output of final results
–m seed  set seed for random generator, >=0
–n nr    set number of random permutations, >=0
–a       generate and test all permutations, overrides –n
–o file  redirect output to file
–x       variance test, –M is ignored
–c       correlation test, –M is ignored
–M file  read matrix file

With no FILE read standard input
```

Then we can test the concordance using standard (prompt line) input:

```
>ptpt –n 5000 <ENTER>
```

the program waits for standard input, we can type a tree with pathogenicity indexes:

```
((((((((1 1)2)2)4)4)2)2)(0 0)) <ENTER>
```

Within seconds we will obtain the results:

```
Results:
Less:           101     2.02%
Equal:          1       0.02%
Greater         4898    98%
```

Alternatively, we can prepare the text file PATHO containing the tree with pathogenicity indexes and then run the test typing the following command:

```
>ptpt -n 20000 PATHO <ENTER>
```

We will obtain practically identical results, 426 (2.13%) less, 3 (0.015%) equal and 19571 (97.9%) greater. The results indicate that there is only approximately 2% probability of obtaining the same or better concordance between pathogenicity of *T. vaginalis* strain and its position within the genealogical tree by chance. Therefore, our experimental data suggest that phylogeneticaly related strains of *T. vaginalalis* express similar pathogenic effects.

Example 2 – Influence of *Toxoplasma gondii* infection on human personality

The program PTPT can also perform the permutation tests analogical to t-test, analysis of variance (ANOVA) and to correlation analysis. The permutation tests can be used for non-normally distributed data and are generally more powerful than analogous non-parametric tests (Manly 1991, Adams & Anthony 1996).

We obtained personality data (Cattell 1970) of 196 women tested for latent toxoplasmosis during gravidity. The average intelligence of 158 *Toxoplasma* free women was 8.3 and of 58 *Toxoplasma* infected ones was 8.9 on a 10-point scale. The results of F-test showed the difference in variances of infected and uninfected subsets (p=0.048). Therefore, the difference in intelligence must be tested with nonparametric tests. The results (p) of Kolmogorov-Smirnov, Wald-Wolfowitz runs test and Mann-Whitney U test were >0.1, 0.023 and 0.076, respectively.

To test the difference in intelligence between toxoplasma infected and toxoplasma free women with PTPT we prepared the text (ASCII) file TOXO.TXT with 196 lines (one line for every subject) containing two numbers, the intelligence and the code of toxoplasmosis status („1“– for toxoplasma free and „2“– for toxoplasma infected).

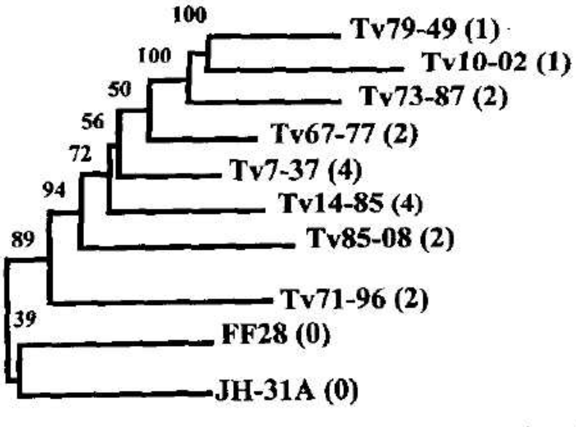

Fig. 1. Phylogenetic tree for ten strains of *Trichomonas vaginalis*. The numbers in parentheses indicate the pathogenicity indexes – Kulda (1989): page 148.

Then we run the program typing a command:

```
>PTPT –n 5000 –x TOXO.TXT <ENTER>
```

Within a minute (using a computer 486DX2, 66 Mhz) we obtained the results:

```
Less:       64     1.22%
Equal:      0      0%
Greater:    4936   98.7%
```

In an agreement with a theory the permutation test was the most powerful from our battery of statistical tests.

Example 3 – The correlation between the duration of toxoplasmosis and the amount of a personality shift

The same data set as in the example 2 was used for testing correlation between duration of chronic toxoplasmosis and amount of the shift of a personality factor A (Sizothymia × Affectothymia) (Cattell 1970). It is known that *Toxoplasma* infected women have significantly higher factor A (higher Affectothymia), i. e., they are more warmhearted, outgoing, easygoing (Flegr et al. 1996). To find out whether the toxoplasmosis induces the increase of the factor A or whether the women with higher factor A have higher probability of *Toxoplasma* infection it was necessary to test the correlation between duration of the infection and the change (decrease) of the factor A. The duration of the infection can be assessed on the basis of decrease of anti-toxoplasma antibodies titre. To test the correlation between the antibody titre we prepared a text file ANTIBODY.TXT with 58 lines containing the factor A and antibody titre for every 58 toxoplasma infected women. Then we run the program typing:

```
>ptpt –n 20000 –c ANTIBODY.TXT
```

Within a minute we obtained the results:

```
Less:       337     1.69%
Equal:      3       0.015%
Greater:    19660   98.3%
```

To eliminate the effect of age of the subjects we can compute age residuals using linear regression between factor A and age of the subject using any statistical program and then preparing the text file RESANTI.TXT containing these residuals instead of factors A. The PTPT analysis of this file provided the results:

```
Less:       245     1.23%
Equal:      0       0%
Greater:    19755   98.8%
```

After elimination of the confounding variable age, the result ($p=0.0123$) was highly significant.

CONCLUSIONS

The program PTPT offers a very powerful and efficient tools for testing a concordance between distribution of phenetic traits and evolutionary history of the taxon. It offers also very powerful tests for statistical analysis of non-normally distributed data. However, with large data sets the time-efficiency of permutation techniques is rather low and rapid computers are necessary to run the analyses. The program PTPT is available at http://www.karlin.mff.cuni.cz/~zaboj/ptpt.

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BOOK REVIEW

MULLIS K. B., FERRÉ F. & GIBBS R. (eds.): **The Polymerase Chain Reaction.** Boston-Basel-Berlin: Birghäuser Verlag, 1994. 458 pp. Format 175×250 mm. Softcover, price sFr 148.–, DM 168.–, Lstg 65.–. ISBN 3–7643–3750–8

This volume presents a comprehensive handbook on polymerase chain reaction (PCR). Edited by Kary Mullis, the inventor of PCR and the Nobel Prize winner in chemistry for 1993, and two prominent experts, this book provides the most up-to-date methodological protocols from the world's leading laboratories. As J. D. Watson emphasizes in the foreword, PCR accelerated substantially the research in the field of molecular biology, and together with the technology of DNA sequencing has had the most extraordinary impact in human genetics. As stated in the preface by K.B. Mullis, since the Symposium on Quantitative Biology in Cold Spring Harbor in 1986, PCR made the research of DNA easy requiring only a few reagents and a cycler. This reaction constitutes an US Patent for amplifying nucleic acid sequences. The list of contributors contains 71 acknowledged reseachers mostly from USA, further on from Finland, France, Germany, Great Britain and Japan. The volume consists of three parts including 35 chapters supplied with numerous tables and with a list of references to the primary literature.

Part one on **Methodology** describing basic laboratory procedures is composed of five sections. First section focuses on manipulation of DNA by PRC, cloning PCR products, optimization of multiplex PCRs, preparation of nucleic acids for archival materials, and PCR amplification. Second section examines problems of quantitation and quantification, following sections are concerned with nonisotopic detection, instrumentation, and sequencing.

Part two on **Application** divided also into two sections, is intended to give insights into in vitro evolution of functional nucleic acids. The application of PCR may be useful in forensic science and in molecular archeology for studies of fossil DNA sequences that are millions years old. PCR may be used also in nonbiological spheres such is the industry. Dramatic technical innovation represents the application of PCR to the study of gene expression, to genetic mapping, population biology and epidemiology. PCR has assumed an important role in the molecular diagnosis of neoplastic, infectious and parasitic diseases and assessment of therapy effectiveness.

Part three covers **PCR and the World of Business**, which includes the place of PCR in the market and a fascinating behind-the-scenes look at the legal battles between biotechnology gigants Cetus and DuPont.

The volume is illustrated by 125 informative figures composed of electrophoreograms, technical equipment, miscellaneous procedures and processes, sequences and diagrams. Each chapter of this unique book will inform the novice and experienced PCR user on how to optimize their results. Every researcher working with PCR will want to own a copy of this book.

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Vertical distribution of soil nematode diversity and abundance in a Central European oak forest

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Abstract. Vertical distribution of soil nematodes to 35 cm depth was studied in a 60–70 year old oak forest on cambisol in South Bohemia for one year. A total of 74 species was found with highest diversity in the humus soil layer 0–5 cm (64 species, 29 constant). 19 species (1 constant) occured in the mineral layer 30–35 cm. No species showed any particular preference for soil layers under 10 cm of soil profile. The mean abundance of total nematode community was 1.19×10^6ind.m^{-2}, the mean biomass 1.25 g.m^{-2}, with peak densities in the December–April period and in August. Abundance and biomass decreased with the depth of soil profile. The nematode community abundance was dominated by *dauer larvae* and bacteriophagous species of the genera *Plectus*, *Acrobeloides* and *Rhabditis*, followed by mycophytophagous nematodes primarily the genus *Filenchus* and for omniphagous nematodes the genera *Eudorylaimus*, *Tylencholaimus* and *Aporcelaimellus*. Phytophagous nematodes were rare. The pattern of nematode vertical distribution studied can be mainly explained by the decrease of humus contents with the depth of soil profile and, consequently, by decreasing microbial activity in deeper soil layers.

Vertical distribution, seasonal changes, oak forest, environmental factors, soil nematodes, Central Europe

Soil nematodes in deciduous forests of the Czech Republic were studied for their diversity, abundance, biomass, and seasonal changes in several localities, mainly in Central Bohemia. Previous forest studies include: a meadow-spruce forest ecotone dominated by oak trees (Háněl 1992–1993); an oak-hornbeam wood (Bartošová & Háněl 1994); oak, oak-hornbeam and beech forests in the Křivoklátsko Biosphere Reserve (Háněl 1996); beech, maple and birch forests of the Velká Kotlina cirque in North Moravia (Háněl 1996a); and an oak forest in Southern Bohemia Háněl (1994). All of these studies of nematodes were conducted in the upper soil layer 0–10 cm because the majority of soil fauna in forest ecosystems occur in the humus horizon (Dunger 1983). Moreover, forest ecosystems in mountain areas are frequently characterized by an abrupt transition between parent rock and shallow humus horizon. The mineral horizon consists of mineral particles in chinks, slits and crevices between boulders so that a quantitative estimate for any group of soil biota is problematic. However, their population densities are generally much lower at depth than those in the upper humus layer. In highlands and lowland forests on cambisols and luvisols, the depth of the soil profile increases and it is not known which proportion of abundance and biomass of soil nematode populations lives in mineral soil below the upper ten centimeters of humus soil. One hypothesis is that the concentration of nematodes in the upper soil layer increases with altitude of the site. For example, Solovyeva (1986) examined nematodes in an altitudinal gradient of the Krymskie Gory Mts (pine and oak forests) from 400 to 1400 m a. s. l., and found that through five 200 m elevations the proportion of nematode numbers in 0–3 cm of the soil profile to that in 3–13 cm increased from an average of 45% to 67%. In other words, the increase in nematode population densities in the upper soil layer at

1400 m a. s. l. accounted for 22% of the total populations as compared to that in 400 m a. s. l. This generalized trend can be dependent on local conditions, for example, alluvial or eolic deposits can support deeper soil profiles in higher altitudes.

The aim of the present study was as follows:

(i) to investigate nematode species distribution in a cambisol soil profile under a sub-climax oak forest

(ii) to estimate nematode abundance and biomass in individual soil layers

(iii) to study seasonal changes of nematode community simultaneously with changes in the soil microclimate, and,

(iv) to relate the pattern of nematode vertical distribution to chemical properties of soil in different depths

MATERIAL AND METHODS

Investigations were carried out from April 1988 to April 1989 in an oak forest of *Quercus robur* L. (60–70 years old) in South Bohemia near Netolice village, 49°04'N, 14°11'E, 486 m a. s. l. (Háněl 1994). Long-term (1900–1950) mean annual air temperature in the region is 7.3 °C, and precipitation 602 mm (50 mm per month in average). Corresponding values in 1988 were 8.2 °C, 623 mm (52 mm), in 1989 8.3 °C, 489 mm (41 mm), and during the study April 1988 – April 1989 8.5 °C, 591 mm (45 mm). Soil samples were taken from 4 walls of a prismatic soil probe dug from square on soil surface with edges of about 40–50 cm to the depth of 35 cm for seven 5 cm deep subsamples in four replicates (layers I–VII). Sampling dates were as follows: 12 April 1988, 10 May 1988, 7 June 1988, 21 July 1988, 10 August 1988, 6 September 1988, 6 October 1988, 8 December 1988, 10 January 1989, 9 February 1989, 14 March 1989, and 4 April 1989. The soil from these subsamples was mixed thoroughly, and a 30 ml subsample was taken for the nematode extraction (Háněl 1994). The rest of the soil was used for moisture, humus and pH analyses.

Soil moisture was measured gravimetrically and expressed as the percentage of H_2O in moist soil. Soil temperature was measured at noon of the sampling dates. Soil temperature was measured in the middle of individual soil layers (i. e. in the layer 0–5 cm at the depth of 2.5 cm, etc.) at each sampling date.

Humus contents of soil layers (percentage of carbon oxydizable by H_2CrO_4, C_{ox}) were measured in May 1988, July 1988, September 1988, December 1988, January 1989, February 1989, March 1989, and in April 1989. pH(H_2O) values were measured in July 1988, September 1988, February 1989, and in April 1989 for each depth.

Pearson correlation coefficients were calculated between the number of species, abundance and biomass on one hand and environmental variables on the other. Redundancy Analysis was performed by the program CANOCO (Ter Braak 1987) defaults and data ln (genus abundance + 1) for samples with complete environmental data in July 1988, September 1988, February 1989, and April 1989 (eigenvalues X1 0.543, X2 0.093, X3 0.052, X4 0.018, percentage variance accounted for these axes 76.0%, 89.0%, 96.2%, 98.9%, respectively).

RESULTS

Abiotic factors

Table 1 shows monthly mean air temperatures, monthly sum of precipitation, sampling time temperature and moisture during the period of investigations. Soil temperatures were separated into: (i) cold period with temperatures lower than 10 °C from December to April and (ii) warm period with temperatures greater than 10 °C from May to October. In the cold period the temperatures were similar in all soil layers, while in the second period the upper soil layers had higher temperatures than the lower ones, especially in May, June and July. Nevertheless, mean temperature values in different soil layers differed only slightly (Table 2). There was little fluctuation in moisture in individual soil layers, although minimum values were observed in October for all soil layers (Table 1). Soil moisture generally decreased with the depth as well as soil carbon contents (Table 2).

Table 1. Monthly mean air temperatures (Temp,°C) and sum of precipitation (Prec, mm) (Part A) and sampling time temperature (°C) and moisture (%) in individual soil layers I–VII (Part B) in an oak forest; layer I: maximum water capacity 64.0–71.1%, pF = 3 at soil moisture of 23.4–27.9%; layer II: maximum water capacity 35.5–38.2%, pF = 3 at soil moisture of 20.5–24.2%

Part A												
	1988								1989			
	Apr	May	Jun	Jul	Aug	Sep	Oct	Dec	Jan	Feb	Mar	Apr
Temp	7.7	13.7	14.7	17.2	17.0	13.0	8.7	1.5	–0.3	2.5	6.6	7.9
Prec	28	45	105	86	72	32	26	53	7	20	11	60
Part B												
Soil temperature												
	1988								1989			
	Apr	May	Jun	Jul	Aug	Sep	Oct	Dec	Jan	Feb	Mar	Apr
I	5.6	13.0	15.0	17.0	18.5	15.2	12.5	4.2	2.4	1.2	5.5	5.3
II	5.5	11.2	12.8	15.3	17.0	15.0	12.3	4.0	2.8	1.2	5.3	5.1
III	5.2	10.5	12.4	14.7	16.8	14.7	11.8	4.0	3.0	1.4	5.0	5.1
IV	5.3	9.8	12.0	14.3	16.5	14.8	11.3	4.2	3.2	1.3	4.5	5.2
V	5.3	9.5	11.5	14.1	16.0	14.6	11.2	4.0	3.2	1.3	5.0	5.3
VI	5.4	9.1	11.3	14.0	16.0	14.6	11.0	4.1	3.3	1.5	4.8	5.4
VII	5.5	9.0	10.0	13.9	15.7	14.6	11.0	4.2	3.4	1.5	4.7	5.5
Soil moisture												
	1988								1989			
	Apr	May	Jun	Jul	Aug	Sep	Oct	Dec	Jan	Feb	Mar	Apr
I	50.4	32.1	37.8	50.1	41.1	54.7	32.0	42.1	59.1	41.6	44.2	46.6
II	25.4	22.4	25.8	30.4	26.3	25.8	14.4	24.8	25.2	25.0	26.3	30.8
III	22.3	17.0	20.9	25.0	21.6	17.9	13.1	20.8	17.6	17.2	20.7	18.8
IV	18.0	18.1	16.8	24.1	19.7	14.6	12.5	19.4	16.5	16.1	14.6	16.7
V	16.8	16.4	14.9	19.0	17.1	13.8	11.6	17.2	15.4	15.0	15.5	15.9
VI	16.3	15.4	14.9	14.5	15.1	11.9	10.8	15.4	15.7	15.4	15.7	14.7
VII	15.6	14.8	18.2	15.4	15.0	11.5	10.5	16.8	16.1	15.1	14.9	14.3

Nematodes

Nematode diversity totaled 74 species and 43 genera. The presence of species in different soil layers is given in Table 3, the abundance of genera in Table 4. The greatest total number of species (64) was in the soil layer 0–5 cm, decreased in 5–10 cm, remained almost stable in 10–30 cm (from 27 to 32), and than decreased to 19 in the layer 30–35 cm. The mean number of species per sample showed a sharp decrease in transition from 5 to 10 cm of soil depth and then gradually declined. The number of constant species in a layer reflected the decrease in mean species number. Consequently, approximately 30 species characterized the nematode community, no species was exclusively characteristic for any soil layer under 10 cm of soil profile. Similar trends were also observed for nematode genera.

The most abundant nematodes belonged to *dauer larvae* (17.1% of the total abundance) and to the genera *Filenchus* (15.8%), *Plectus* (13.5%), *Acrobeloides* (11.4%), *Rhabditis* (8.9%), *Eudorylaimus* (7.9%), *Tylencholaimus* (4.5%), and *Aporcelaimellus* (4.1%). The species of those dominant genera occupied all soil layers, except for *Aporcelaimellus* which genus was not recorded in the soil layer 30–35 cm. Some species of less dominant genera also occurred throughout all soil layers, mainly those of *Alaimus* and *Clarkus*. The genera *Eumonhystera*, *Geomonhystera*, *Cylindrolaimus*, *Ceratoplectus*, *Wilsonema*, *Tylocephalus*, *Teratocephalus*, *Bastiania*, *Lelenchus*, *Cephalenchus* were mostly limited to the humus layer 0–5 cm.

Table 2. Mean values of environmental variables in individual soil layers I – VII in an oak forest
1)according to Novák (1992)
2)according to Kalčik & Šanrůčková (1994)

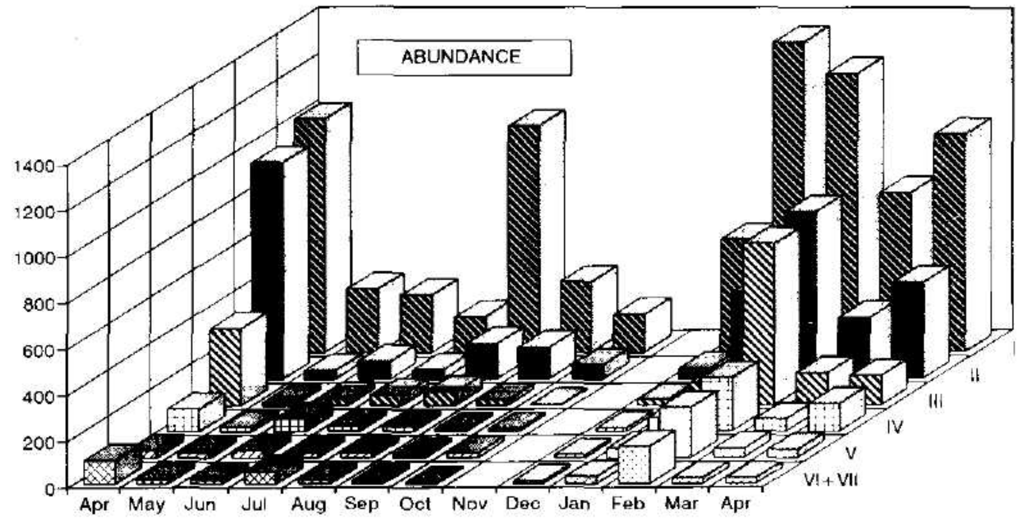
	I	II	III	IV	V	VI	VII
Temperature (°C)	9.6	9.0	8.7	8.5	8.4	8.4	8.3
Moisture (%)	44.3	25.2	19.4	17.3	15.7	14.7	14.9
C_{ox} (%)	12.2	2.3	1.1	0.9	0.6	0.6	0.5
N_{total} (%) 1)	2.0	0.5	0.2	0.2	0.2	0.2	0.2
P_{total} ($mg.kg^{-1}$) 2)	557	470	442	442	418	418	398
$P_{mineral}$ 2)	389	382	346	346	340	340	348
$P_{organic}$ 2)	168	88	96	96	78	78	50
$P_{microbial}$ 2)	64	20	23	23	24	24	9
pH(H_2O)	5.0	4.2	4.3	4.4	4.5	4.7	4.7

Mean total abundance of nematodes for all soil layers in the investigated period was 1193×10^3ind.m^{-2} and varied from 268 (October 1988) to 3220 (February 1989) $\times10^3$ind.m^{-2}. A remarkable peak of abundance was observed in the cold period, i. e. from December to April, the second peak occurred in August (Fig. 1). Nevertheless, this summer peak was caused by nematode populations increase in the soil layer 0–5 cm whereas the winter-early spring population maxima also occurred in the soil layers 5–10 cm and 10–15 cm (Fig. 1). Mean abundance of nematodes decreased with the depth of soil profile and it can be generalized that a lower layer had a twice lower number of nematode individuals than the upper one (or Total Abundance = $\Sigma A(n=1)/2^{n-1}$, $A(n=1)$ is abundance in the first soil layer). Abrupt decrease of nematode abundance was especially observed in the orders Dorylaimida, Araeolaimida and Mononchida. Nematodes of the orders Rhabditida and Tylenchida reached high population densities in deeper soil layers, too. Proportion of adult nematodes in individual soil layers varied from 15.7% to 28.3%, in average, adults constituted about 22.1% of the total populations (Table 4).

Mean total biomass of nematodes was 1245 mg.m^{-2} with seasonal fluctuations from 369 (Jun 1988) to 3012 (February 1989) mg.m^{-2}. As seen in Fig. 1, the greater part of nematode biomass was concentrated in the soil layer 0–5 cm. In August and in January–February, there were two peaks of biomass, April was characterized by a decrease in nematode biomass in both years. This distribution of nematode biomass reflected nematode abundance and the fact that the humus soil layer (0–5 cm) was inhabited by big nematode specimens as summarized in the high mean biomass of a nematode individual (1.77 μg) in this layer (Table 4).

Mean total abundance, biomass, numbers of species and genera of nematodes in the soil layers investigated significantly increased with increasing values of soil moisture, temperature, carbon, nitrogen, and all forms of phosphorus ($r = 0.76$–0.99; $P = 0.05$–0.01, $n = 7$). No significant correlation was found between these characteristics and pH values. The same was true for the abundance of the orders Teratocephalida, Tylenchida, Enoplida, and Dorylaimida; Monhysterida, Araeolaimida, Alaimida, and Mononchida were not significantly correlated with mineral phosphorus. Rhabditida were not significantly correlated with carbon, mineral and organic phosphorus, they had negative but insignificant correlation with vertical changes of pH values. Aphelenchida were significantly positively correlated with vertical distribution of soil moisture, temperature, carbon, and total and mineral phosphorus. Percentage of adult specimens was significantly negatively correlated with pH ($r = -0.82$, $P = 0.05$, $n = 7$).

Any significant correlation was found neither in total values nor in individual soil layers between air temperature or precipitation and seasonal changes of abundance and biomass, although correlation coefficients were mostly negative. In individual soil layers, abundance of nematodes was significantly negatively correlated with sampling time temperature through 0–20 cm of soil profile (r = –0.59 – –0.66, P = 0.05, n = 12) but no significant correlation was found between abundance and sampling time moisture. No significant correlation was between sampling time temperature or sampling time moisture and corresponding biomass values in individual soil layers.



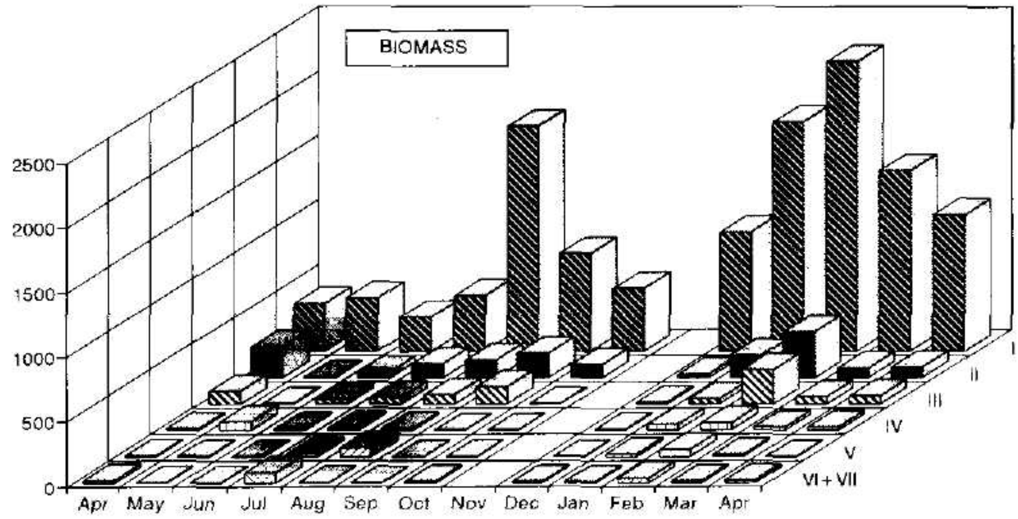


Fig. 1. Seasonal changes of nematode abundance ($\times 10^3$ind.m^{-2}) and biomass (mg.m^{-2}) in individual soil layers I–VII in an oak forest.

Table 3. Presence of soil nematodes in different soil layers in an oak forest, * indicates constant species (constancy >= 50%) in a layer

	I	II	III	IV	V	VI	VII
order: MONHYSTERIDA							
1 *Eumonhystera vulgaris* (de Man, 1880)	+					+	
2 *Eumonhystera longicaudatula* Gerlach & Riemann, 1973)	+						
3 *Geomonhystera villosa* (Bütschli, 1873)	+						
order: ARAEOLAIMIDA							
4 *Cylindrolaimus bambus* Andrássy, 1968	+						
5 *Plectus acuminatus* Bastian, 1865	*	*	+	+	+	+	+
6 *Plectus geophilus* de Man, 1880	+						
7 *Plectus longicaudatus* Bütschli, 1873	*	*	+	+	+	+	
8 *Plectus parvus* Bastian, 1865	*	+	+	+	+	+	+
9 *Plectus rhizophilus* de Man, 1880		+	+	+			+
10 *Plectus sambesii* Micoletzky, 1915	+	+					
11 *Plectus silvaticus* Andrássy, 1986	*			+	+	+	
12 *Ceratoplectus assimilis* (Bütschli, 1873)	+						
13 *Ceratoplectus armatus* (Bütschli, 1873)	*						
14 *Wilsonema otophorum* (de Man, 1880)	+	+					
15 *Tylocephalus auriculatus* (Bütschli, 1873)	+						
order: TERATOCEPHALIDA							
16 *Metateratocephalus crassidens* (de Man,1880)	+	+	+				
17 *Teratocephalus stratumus* Eroshenko, 1973	+	+	+				
18 *Teratocephalus tenuis* Andrássy, 1958	+						
19 *Teratocephalus terrestris* (Bütschli, 1873)	+						
order: RHABDITIDA							
20 *Heterocephalobus elongatus* (de Man, 1880)	*	+	+				
21 *Heterocephalobus loofi* Andrássy, 1968	*	+			+		
22 *Cephalobus persegnis* Bastian, 1865		+					
23 *Cephalobus troglophilus* Andrássy, 1967	*	+				+	
24 *Eucephalobus oxyuroides* (de Man, 1876)	+	+					
25 *Acrobeloides nanus* (de Man, 1880)	*	*	*	*	*	*	*
26 *Panagrolaimus rigidus* (Steiner, 1866)	+			+		+	+
27 *Bursilla monhystera* (Bütschli, 1873)	*	+	+	+			
28 *Rhabditis maupasi* group Seurat in Maupas, 1919	*	*	*	*	*	*	+
29 *dauer larvae*	*	*	*	+	*	+	+
order: DIPLOGASTERIDA							
30 *Diplogaster* Schultze in Carus, 1857 sp.	+					+	
order: APHELENCHIDA							
31 *Aphelenchus avenae* Bastian, 1865	+	+					
32 *Aphelenchoides saprophilus* Franklin, 1957	+				+		
33 *Aphelenchoides* Fischer, 1894 sp.	*	+	+				
34 *Aphelenchoides ferrandini* Meyl, 1954	*	+	+	+			
order: TYLENCHIDA							
35 *Filenchus amaritus* Zell, 1988	+	+					
36 *Filenchus discrepans* (Andrássy, 1954)	+	+		+	+	+	
37 *Filenchus helenae* (Szczygiel, 1969)	+	+	+	+	+	+	
38 *Filenchus longicaudatulus* Zell, 1988	+	+	+	+			
39 *Filenchus minutus* (Cobb, 1893)	*	*	+	+	+	+	+
40 *Filenchus vulgaris* (Brzeski, 1963)	+		+			+	
41 *Aglenchus agricola* (de Man, 1884)				+			+
42 *Malenchus acarayensis* Andrássy, 1968 and 43 *Malenchus bryophilus* (Steiner, 1914)	*	+				+	+

	I	II	III	IV	V	VI	VII
44 *Lelenchus leptosoma* (de Man, 1880)	+						
45 *Cephalenchus megacephalus* Goodey, 1962	+						
46 *Paratylenchus projectus* Jenkins, 1956		+		+	+		
47 *Ditylenchus* (Filipjev, 1936) sp.1 and 48 *Ditylenchus* (Filipjev, 1936) sp.2	+	+	+	+		+	
order: ENOPLIDA							
49 *Bastiania gracilis* de Man, 1876	+						
50 *Prismatolaimus dolichurus* de Man, 1880	+				+	+	+
51 *Prismatolaimus intermedius* (Bütschli,1873)	*		+	+	+		+
52 *Tripyla filicaudata* de Man, 1880	+	+		+	+		+
53 *Tobrilus* Andrássy, 1959 sp.			+				
order: ALAIMIDA							
54 *Alaimus parvus* Thorne, 1939	*	+	+	+	+	+	+
55 *Alaimus primitivus* de Man, 1880	+						
order: MONONCHIDA							
56 *Clarkus papillatus* (Bastian, 1865)	*	+	+	+	+	+	+
57 *Prionchulus punctatus* (Cobb, 1917)	*	+	+		+	+	
58 *Anatonchus tridentatus* (de Man, 1876)					+		
order: DORYLAIMIDA							
59 *Nygolaimus* Cobb, 1913 *sp.*							+
60 *Mesodorylaimus bastiani* (Bütschli, 1873)	*	+		+		+	
61 *Eudorylaimus carteri* (Bastian, 1865)	*	+	+	+		+	+
62 *Eudorylaimus paucipillatus* Andrássy, 1986	*	*			+		
62 *Eudorylaimus parvus* (de Man, 1880)	*	*	*	+	+	+	+
64 *Eudorylaimus silvaticus* Brzeski, 1960	*	+	+	+			
65 *Thonus ettersbergensis* (de Man, 1885)	*	+			+	+	
66 *Thonus* Thorne, 1974 sp.	+				+		
67 *Aporcelaimellus obscurus* (Thorne et Swanger, 1936)	*	*	*	+	+	+	
68 *Pungentus thornei* Goodey, 1943			+	+	+	+	
69 *Tylencholaimus minimus* de Man, 1876	+			+		+	
70 *Tylencholaimus mirabilis* (Bütschli, 1873)	*	*	+	+	+	+	
72 *Tylencholaimus stecki* Steiner, 1914	*	+	+	+			+
73 *Diphtherophora* de Man, 1880 sp.						+	
74 *Trichodorus* Cobb, 1913 sp.	+						

Total number of species was significantly negatively correlated with air temperature (r = –0.80, P = 0.01, n = 12) and with precipitation (r = –0.66, P = 0.05, n = 12). As concerns individual soil layers, the number of species was significantly negatively correlated with soil temperature in the layer 0–5 cm (r = –0.85, P = 0.01, n = 12) and in the layer 5–10 cm (r = –0.80, P = 0.01, n = 12). No significant correlation was between species number and soil moisture.

In the layer 0–5 cm, seasonal changes in nematode abundance and biomass were positively but not significantly correlated with soil carbon (r = 0.61 and r = 0.43, respectively, n = 8). In deeper layers, correlation coefficients were also insignificant, positive or negative. The same was true for species number.

Abundance and species number were negatively correlated with pH in the layer 0–5 cm (r = –0.97 and r = –0.99, respectively, n = 4). Negative correlations were also in the layer of 5–10 cm but of lower values (r = –0.37 and r = –0.47, respectively, n = 4) whereas under 10 cm of the soil profile correlation coefficients were positive. However the number of four replicates is too low for precise conclusion, relatioships between nematodes and soil acidity in the layer 0–5 cm differed from those in deeper layer, the layer 5–10 cm being an transitional zone because of an abrupt decrease in pH values (Table 2).

In summary, seasonal changes in cumulative characteristics of nematodes such as species number, abundance, and biomass in the most populated soil layer 0–5 cm were positively (but not significantly) correlated with total soil carbon. As concerns air temperature, precipitation, soil temperature, soil moisture, and soil pH the correlation coefficients were significantly negative or insignificant in absolute values. In other words, low values (in seasonal changes and in the established range) of these five parameters had no negative serious effects on total diversity or on total population densities of nematodes.

Nevertheless, the effect of those parameters was detectable in composition of nematode assemblages in individual soil layers. High positive correlations of soil carbon and soil moisture with the first ordination axis (Table 5) reflected population composition in the soil layer 0–5 cm with high population densities of the genera *Plectus*, *Aporcelaimellus*, *Eudorylaimus* (Fig. 2). Negative correlation with the soil depth showed its negative influence upon nematode populations because they related to samples with low population densities in deeper parts of soil profile. Weak correlation with ordination axes was established for pH of soil. As to the temperature, we could expect a greater but ambiguous effect on the composition of nematode assemblages in the layers studied (negative correlation with the first ordination axis, positive with the second one).

DISCUSSION

The composition of the nematode community in the investigated period was similar to that found during previous investigations (Háněl 1994, 1995). Dominant nematodes belonged to the genera *Plectus*, *Acrobeloides*, *Rhabditis*, *dauer larvae*, *Filenchus*, *Eudorylaimus*, *Tylencholaimus*. In the soil layer 0–10 cm, mean abundance was 921×10^3ind.m^{-2} and biomass 1118 mg.m^{-2} with peaks in the January–April and August periods and these data are comparable with those obtained in 1986–1987.

As shown in the present study, approximately 77% of nematode individuals and 90% of nematode biomass occurred in the layer 0–5 cm, correlated with soil moisture and humus contents. This general trend corresponds with many results established by other authors. Pick-Hong (1966) found that in deciduous mixed woodland habitats in England nematodes were most abundant in the soil layer 0–2 cm and their numbers (as well as soil moisture) decreased with decreasing depth of soil profile down to 24 cm. Razzhivin (1976) studied nematodes of various ecosystems in Alatau and found maximum abundance in the soil layer 1–10 cm. Pavlyuk (1983) found the majority of nematodes in litter, then in humus A-horizon, while mineral B-horizon was inhabited by negligible numbers of individuals in a birch wood in the Moscow region. Popovici (1984) estimated 74.2% of nematode abundance in the soil layer 0–10 cm (including litter) whereas 25.8% occurred in the layer 10–15 cm.

Although the total abundance usually decreases with soil depth, different species or genera can prefer different parts in soil profile and influence the pattern of nematode vertical distribution at individual stands. Popovici (1980) studied vertical distribution of nematodes in various ecosystems in the Western Carpathians in Rumania. The majority of nematode species concentrated in litter, F- and H-horizons and in the first mineral (humiferous) horizon. Nevertheless, preference for different soil layers was observed in some species. For example, the species of the

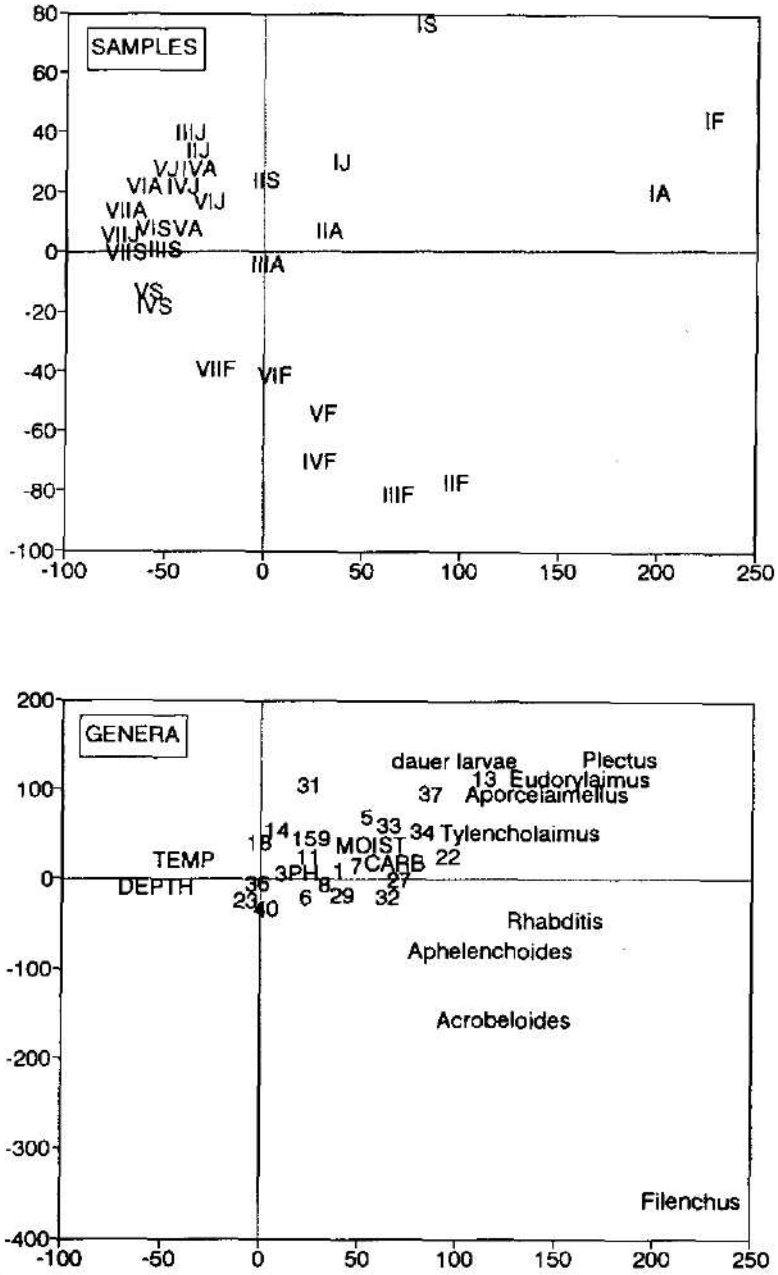


Fig. 2. Ordination of samples and genera of soil nematodes in individual soil layers I–VII; J = July 1988, S = September 1988, F = February 1989, A = April 1989; biplot scores of environmental variables TEMP = soil temperature, MOIST = soil moisture, CARB = C_{ox}, PH = pH(H_2O), DEPTH = depth of soil; explanation for nematode genera numerals see Table 4.

Table 4. Mean abundance ($\times 10^3$ind.m^{-2}) of soil nematode genera in different soil layers in an oak forest and cumulative characteristic of nematode community, + indicates abundance lower than 1000 ind.m^{-2}

	I	II	III	IV	V	VI	VII	SUM
order: MONHYSTERIDA								
1 *Eumonhystera* Andrássy, 1981	4					+		4
2 *Geomonhystera* Andrássy, 1981	+							+
Σ	4					+		4
order: ARAEOLAIMIDA								
3 *Cylindrolaimus* de Man, 1880	+							+
4 *Plectus* Bastian, 1865	130	12	6	4	3	3	1	161
5 *Ceratoplectus* Andrássy, 1984	12							12
6 *Wilsonema* Cobb, 1913	1	+						1
7 *Tylocephalus* Crossmann, 1833	2							2
Σ	145	13	6	4	3	3	1	176
order: TERATOCEPHALIDA								
8 *Metateratocephalus* Eroshenko, 1973	1	+	+					2
9 *Teratocephalus* de Man, 1876	3	+	+					4
Σ	4	1	1					6
order: RHABDITIDA								
10 *Acrobeloides* (Cobb, 1924)	50	45	18	10	7	4	3	136
11 *Cephalobus* Bastian, 1865	6	2				+		8
12 *Eucephalobus* Steiner, 1936	+		+					+
13 *Heterocephalobus* (Brzeski, 1960)	15	2	+		+			17
14 *Panagrolaimus* Fuchs, 1930	1			+		+	+	2
15 *Bursilla* Andrássy, 1976	10	1	+	+				11
16 *Rhabditis* Dujardin, 1845	58	23	9	5	8	3	1	106
17 *dauer larvae*	39	107	35	17	4	2	+	204
Σ	179	178	62	32	20	10	4	485
order: DIPLOGASTERIDA								
18 *Diplogaster* s.l. Schultze in Carus, 1857	+					+		1
Σ	+					+		1
order: APHELENCHIDA								
19 *Aphelenchus* Bastian, 1865	+	+						+
20 *Aphelenchoides* Fischer, 1894	13	10	1	+	+			24
Σ	13	11	1	+	+			25
order: TYLENCHIDA								
21 *Filenchus* (Andrássy, 1954)	55	47	49	14	12	9	4	189
22 *Malenchus* Andrássy, 1968	20	+				+	+	22
23 *Aglenchus* (Andrássy, 1954)				+			+	+
24 *Cephalenchus* (Goodey, 1962)	+							+
25 *Lelenchus* (Andrássy, 1954)	+							+
26 *Paratylenchus* Micoletzky, 1922		+		+	+			1
27 *Ditylenchus* Filipjev, 1936	10	1	+	1		+		12
Σ	86	49	49	15	12	10	4	224
order: ENOPLIDA								
28 *Bastiania* de Man, 1876	1							1
29 *Prismatolaimus* de Man, 1880	4		1	+	+	+	+	6
30 *Tobrilus* Andrássy, 1959			+					+
31 *Tripyla* Bastian, 1865	9	3		+	+		+	12
Σ	14	3	1	+	1	+	1	19
order: ALAIMIDA								
32 *Alaimus* de Man, 1880	6	+	1	+	2	+	+	9
Σ	6	+	1	+	2	+	+	9

	I	II	III	IV	V	VI	VII	SUM
order: MONOCHIDA								
33 *Clarkus* Jairajpuri, 1970	7	1	+	1	1	1	+	10
34 *Prionchulus* (Cobb, 1916)	10	+	+		+	+		11
35 *Anatonchus* (Cobb, 1916)					+			+
Σ	17	1	1	1	1	1	+	21
order: DORYLAIMIDA								
36 *Nygolaimus* Cobb, 1913					+			+
37 *Mesodorylaimus* Andrássy, 1959	21	+		+		+		22
38 *Eudorylaimus* Andrássy, 1959 s.l.	82	6	3	2	1	+	+	94
39 *Aporcelaimellus* Heyns, 1965	38	6	4	1	1	+		49
40 *Pungentus* Thorne et Swanger, 1936			+	1	+	+	+	2
41 *Tylencholaimus* de Man, 1876	41	5	2	3	1	2		54
42 *Trichodorus* Cobb, 1913	+							+
43 *Diphtherophora* de Man, 1880						+		+
Σ	182	18	9	6	3	4	1	222
TOTAL ABUNDANCE [$\times 10^3$ ind.m^{-2}]	650	272	131	60	41	29	12	1193
TOTAL BIOMASS [mg.m^{-2}]	989	128	69	23	17	15	4	1245
MEAN INDIVIDUAL BIOMASS [μ g]	1.77	0.81	1.07	0.64	0.54	0.95	0.43	
TOTAL NUMBER OF SPECIES	64	42	32	32	27	32	19	
NUMBER OF CONSTANT SPECIES	29	10	5	2	3	2	1	
MEAN NUMBER OF SPECIES	27	11	7	6	5	5	3	
TOTAL NUMBER OF GENERA	36	24	21	20	18	21	15	
MEAN NUMBER OF GENERA	20	9	7	6	5	5	3	
PERCENTAGE OF ADULT INDIVIDUALS	27.9	19.9	15.7	20.5	18.4	28.3	24.2	22.1

genera *Cephalobus, Bunonema, Plectus, Teratocephalus, Monhystera, Criconema, Ecphyadophora* showed a distinct preference for upper soil layers to 15 cm depth. The species of *Tripyla, Clarkus, Eudorylaimus, Filenchus* were prevalent between 10–40 cm in soil profile, while the species of *Trichodorus, Tylolaimophorus, Diphtherophora, Gracilacus, Miconchus*, and *Longidorus* were identified in deeper soil layers from 30 to 100 cm. Nothing like that was experienced for the forest nematodes studied. Of the total 74 species 7 (9.5%) were not recorded in the layer 0–10 cm (*Aglenchus agricola, Pungentus thornei, Nygolaimus* sp., *Anatonchus tridentatus, Tobrilus* sp., *Diphtherophora* sp.) and only one (*Tobrilus* sp.) was not found in this layer during 1986–1987 (Háněl 1994). Clearly, the effectiveness of species sampling in the layer 0–10 cm was almost hundred percent and all species characterizing the nematode community studied were constant in upper soil layers.

As concerns other localities, Šály (1973) studied nematodes down to the depth of 120 cm in an oak-hornbeam forest at Nitra (Slovakia). He found 16 (27.1%) species which did not occurr in the upper soil layer 0–12 cm, nevertheless, none belonged to dominants and accounted altogether only for 2.5% of total nematode numbers. Vertical distribution pattern of population densities was different from that in the oak forest studied as only 47.6% of nematode individuals inhabited the 0–12 cm layer and the decrease of abundance with the depth of soil profile was less precipitous.

Brzeski (1989) investigated vertical distribution of soil nematodes in six deciduous forests (May 1985) of the Mazovian Lowland in Poland and he distinguished litter, humus layer (2–15 cm) and mineral layer (to the 25–30 cm of soil profile). Total number of species at individual sites varied from 33 to 51, the number of species recorded exclusively in the mineral layer varied from 0 to 8 (i. e. 0–17.0% of the overall species richness). Considering abundance, the mineral layer was inhabited by 0.5–8.2% of the total of nematode individuals, the litter was occupied by 50.3–97.3% of individuals, consequently, his data can accord well with the data of the present study.

A phenomenon has to be stressed here. In the oak forest studied, as well as in the deciduous forests studied by Brzeski (1989), nematode parasites of higher plants accounted for a negligible proportion of total nematode populations and nematode abundance and biomass concentrated in litter-humus layers. Brzeski (1989) stated that „the quantity of available food, as well as air and water relations, are the tentative cause of the vertical differentiations of the nematode fauna" and that „most of nematodes found are microbial feeders". These conclusions are also applicable to the vertical distribution of nematodes in the oak forest studied. On the other hand, plant-parasitic nematodes (Hoplolaimidae, Dolichodoridae, Criconematodae, Longidoridae) represented 17.3% of total community abundance in the oak-hornbeam forest studied by Šály (1973) and reached high population densities in deeper soil layers 12–120 cm. It can be hypothesized that in Central Europe deciduous forest ecosystems the proportion of nematode individuals in soil layers under 10 cm increases with increasing population densities of parasitic nematodes feeding upon tree/shrub roots. Under such circumstances, we can possibly find abundance peaks (at least for some species) at various depths of soil profile. These peaks are not to concern exclusively phytophagous nematodes, destroyed and decaying roots can stimulate patches of microbial activity and, consequently, higher population densities of nematode species feeding on soil microflora (and nematode predators and parasites). If a nematode community is mainly characterized by microbial feeders species, populations concentrate in litter and humus horizons and total abundance gradually or abruptly decreases with the depth of soil profile. This can be supported by the results of Wasilewska (1974). She sampled soil nematodes down to the depth of 50 cm in two pine-juniper-oak woods, 10-year-old and 17–20-year-old, in Poland (July 1971). In the layer 0–10.5 cm, 32.8–62.1% of the total abundance and 23.8–61.9% of the total biomass were found because many parasites of higher plants and omnivorous nematodes reached a high abundance in deeper soil layers. Microbivorous nematodes, however, were densest in the top layer.

Vertical distribution of nematodes was significantly positively influenced by quantities of all soil abiotic factors studied as given in Table 2, except for pH(H_2O) which values were significantly negatively correlated with the percentage of adult specimens. It is difficult to explain this phenomenon but low pH might prevent nematode juveniles from maturation in the cambisol successional row studied. Háněl (1995) found higher soil pH values in cultivated field, fallow and meadow than in oak forest simultaneously with a lower percentage of adults in this forest. A causal explanation could be that lower pH values negatively affect bacteria (Myrold 1990) and, consequently, complicate recovery of rhabditid bactriophagous nematodes from dauer stage and maturation, responding this way to metabolites of growing bacterial populations (Golden & Riddle 1984). In the forest studied, nematodes of the order Rhabditida were abundant in the layer 5–10 cm, whereas Araeolaimida strictly preferred the layer 0–5 cm (Table 4). *Dauer larvae* in the forest studied represented non-feeding stages of rhabditid nematodes, considering their morphology and anatomy (Poinar 1986, Weiser & Mráček 1988), in greater part those of the family Steinernematidae. Fischer & Führer (1990) found that soil with pH levels below 4.0 may limit host-finding by entomophilic free-living stages of *Steinernema*, i. e. their maturation. This can also explain a part of high population densities of *dauer larvae* in the soil layer 5–10 cm (Table 4) with the lowest pH value (Table 2). At the pH soil value 6.9, Koppenhöfer et al. (1995) found a uniform distribution of infective steinermatid juveniles in soil. On the other hand, the highest values of abundance and biomass of nematode community were in cold winter-early spring period with lower values of pH 4.8–5.0 than in warm summer-autumn period

Table 5. Correlation coefficients of soil environmental variables with ordination axes of nematode genera

	X1	X2	X3	X4
Soil temperature	–0.51	0.58	0.08	–0.27
Soil moisture	0.74	0.49	0.16	0.02
C_{ox}	0.79	0.45	–0.11	–0.04
pH(H_20)	0.28	0.17	–0.59	0.30
Depth of soil	–0.69	–0.22	–0.41	0.02

with pH 5.1–5.2 in the soil layer 0–5 cm. Evidently, pH ranging around the value of 5.0 exerted no inhibitory effect on nematode development as can be compared with pH values of about 4.0 in deeper soil layers.

Soil carbon, moisture and temperature are mentioned as abiotical factors, nevertheless, humus is of biological origin and the ability of soil to hold water and to conduct heat is substantially influenced by soil biological activity. Háněl (1994) proposed that „seasonal changes in population densities of nematode species in the oak forest studied resulted from biological interactions in soil and, to a less extent, from moisture-temperature fluctuations“. As the composition and seasonal changes of nematodes observed in 1988–1989 confirmed results reported previously, this topic can be discussed in details.

Balík (1989) investigated soil testate amoebae down to the depth of 10 cm in the oak forest simultaneously with Háněl's (1994) study on nematodes and found that 68.7% of the individuals lived in the soil layer 0–5 cm. Population maxima of testate amoebae (56–72×10^3ind.cm^{-2}) were observed in the May–June period and these abundance peaks preceded those of nematodes in August. In the winter period, however, the abundance of testate amoebae was twice to three times lower than in early summer peaks. This might be due to the competition among some groups of nematode and testate amoebae species. It is also known that nematodes can feed on protozoans (Small 1987) and testate amoebae can be predators of nematodes (Yeates & Foissner 1995).

Šantrůčková (1992) studied microbial biomass, activity and soil respiration in 1987–1988 and the values of these characteristics were evidently higher in humus horizon than in mineral horizon. In the layer 0–5 cm, peaks of microbial biomass appeared during the cold (winter October–April) period as well as in the warm (summer July–August) period, separated by distinct minima. This pattern of changes in microbial biomass coincided well with seasonal changes of nematode abundance as observed from 1986 to 1989 and indicated that a greater deal of nematode populations were microbial feeders.

Tajovský et al. (1992) studied decomposition of faecal pellets of the millipede *Glomeris hexasticha* and relationships between nematodes and physiological groups of soil microorganisms during the 1987–1988 period. Certain nematode genera were significantly positively correlated with the groups of microflora as follows: *Rhabditis* with heterotrophic bacteria, *Aporcelaimellus* and *Clarkus* with oligotrophic bacteria, *Filenchus*, *Cephalobus*, *Malenchus*, *Mesodorylaimus*, *Prismatolaimus*, and *Heterocephalobus* with amylolytic actinomycetes, *Plectus*, *Acrobeloides*, *Aphelenchoides*, *Prionchulus*, *Metateratocephalus*, *Bunonema*, *Ceratoplectus*, *Tylencholaimus*, and *Filenchus* with chitinolytic actinomycetes. The genera listed above mostly belong to microbivorous trophic groups inclusive omniphages partially or probaly completely (e. g. *Tylencholaimus*) feeding on microflora. Predarory nematodes of the order Mononchida can feed on bacteria, too (Yeates 1987). Decomposing excrements of millipedes (arthropode moder) considerably contribute to the formation of humus horizon in the oak forest studied so that relatioships between soil mikro-mesofauna including nematodes and humus-forming microflora are no surprise. Down to the depth of soil profile humus contents decrease simultaneously with decreasing populations of soil microflora and fauna. A barrier for some species can also be a lower pH values zone in the soil layer 5–15 cm as found in the present study, previously reported by Kalčik & Šanrůčková (1994) and discussed above.

Seasonal changes of total abundance and biomass of nematodes were negatively but insignicantly correlated with either precipitation or air temperature, the number of species was singificatly negatively correlated with both mentioned factors. Considering weak correlations between those nematode characteristics and soil moisture and temperature in individual soil layers, we can conclude that soil microclimate had a low influence on nematodes in general. Nematodes here were probably well adapted to relatively low soil temperatures. Table 2 shows that mean sampling time temperatures were about 8 to 10 °C, therefore, temperature was no limiting factor to nematodes in this site during the period investigated. For example, Trudgill (1995) gives minimum base temperatures for development of free-living and plant-parasitic nematodes from 0.9 °C to 13.1 °C, mostly being lower than 10 °C. The same seems to be true for soil moisture. In fact, soil moisture never decreased under values corresponding to pF 3 in the layer 0–5 cm as well as in the layer 5–10 cm (except for October 1988), Demeure et all. (1979) found pF values 3–6 to be initiating nematode anhydrobiotic coiling. On the other hand, Šantrůčková (1992) found microbial biomass to be significantly positively correlated with soil moisture. Positive correlation between nematode abundance (biomass) and soil carbon in the soil layer 0–5 cm was established in the present study. During the decompostion of millipede excrements (Tajovský et al. 1992) the nematode abundance reached peak in November (coinciding with peaks in population densities of oligonitrofil bacteria and chitinolytic actinomycetes), the nematode biomass consecutively in April (coinciding with peaks of oligotrophic bacteria, amylolytic actinomycetes, and partially of micromycetes). The peak in both abundance and biomass of testate amoebae appeared in August and then their populations declined. Again, the peak of testate amoebae preceded the increase in nematode populations as previously reported for their mean soil abundance in 1986–1987. Soil moisture probably stimulates a quick increase in microbial population. Some populations of protozoans consequenly increase their abundance and biomass. Nematodes can quickly recover from anhydrobiosis or draught-induced quiescence. Nevertheless, their generation cycles are usually longer than those of protozoan and soil microflora and peak in nematode populations, grazing on multiplicating protists, postpones.

As revealed by ordination analysis, higher humus contents and higher moisture in soil can explain the dominance of nematodes such as *Plectus*, *Eudorylaimus*, *Aporcelaimellus*, *Tylencholaimus*, and *dauer larvae* (Fig. 2B) being in greater part microbial feeders. No analyzed factor can be directly related to the distribution of other dominant nematodes, i. e. *Filenchus*, *Acrobeloides*, *Rhabditis*, and subdominant *Aphelenchoides*. Three lately named genera are typical microbial feeders and the same is very likely true for Filenchus in the forest studied, too. Newertheless, their distribution is less dependent on higher humus amounts than on instantaneous microbial activity. The first group needs humous soil as their habitat beside available populations of microorganisms – this also follows from their distribution in successional stages (Háněl 1995). Missing environmantal variable for the sector of ordination space delimited by positive X1 values and negative X2 values was probably microbial activity (or its part). This gap is challenging to further research.

CONCLUSIONS

Soil nematodes in the oak forest studied mainly inhabited the humus layer 0–5 cm, down to the depth of the soil profile species number, abundance, and biomass decreased. The conventionally sampled 0–10 cm of soil were occupied by 90% of species recorded in this study and 77% of nematode individuals representing 90% of total nematode biomass. Of the dominant genera, *Plectus*, *Eudorylaimus*, *Tylencholaimus*, *Aporcelaimellus*, and partially *Rhabditis* evidently preferred the layer 0–5 cm, *dauer larvae*, *Acrobeloides* and *Filenchus* also reached high population densities in the layer 5–10 cm. Main factors governing nematode vertical distribution seemed to be humus contents and microbial activity in soil. Seasonal fluctuations in soil moisture and temperature were no limiting factor to nematodes, nevertheless, low values of soil pH could have an inhibitory effect on population development of some nematodes in the layer 5–10 cm.

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Incidence of protogynous and protandrous development in the pre-imaginal stage of insect development: an overview

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Abstract. The sex-related variation in the relationship between temperature and developmental time in larvae, pupae and complete development of 97 non-diapausing species of insects is reviewed. The frequency of protandry and protogyny, the magnitude of differences and their importance relative to other sources of variation in developmental time were considered. There exist 6 temperature/developmental time relationships: protandric or protogynic development with monotonous increase or decrease in the difference between the sexes with temperature, and development that switches from protandry to protogyny, or *vice versa*. The differences were recorded at a range of temperatures, from 5 °C above the lower development threshold to +30 °C. Protandry prevailed in larval (64% of all cases) and complete development (43%) and protogyny was rare (7 and 18%, resp.). Protogyny was commoner in pupal development (46%). Development with a switch between protandry and protogyny and *vice versa* occurred in 29% of the larval, 26% of the pupal and 38% of the complete developments. Due to the distribution of the temperatures for switching between protandry and protogyny over the range 10–30 °C, the proportion of insects showing protandry in larval development increased with increasing temperature from ca 45% to ca 85%, but remained relatively stable for pupal development, between ca 35–45%. The proportion showing protandry in complete development increased slightly, from ca 55% to ca 70%. Not unexpectedly, the differences between the developmental time of both sexes expressed in days decreased with increasing temperature, and when expressed as a percentage of the developmental time of the slower growing sex they were similar for all temperatures. Theory predicts that protandry may sometimes have an adaptive significance. This was tested by comparing the relative importance of the differences in developmental time due to sex with the individual variation in development time in several randomly selected species. The differences in development time due to sex were mostly less important than individual variation. Only a small proportion of the differences due to sex could be ecologically significant.

Development length, temperature, sex-related variation, male, female

INTRODUCTION

It is well known that both in the field and in the laboratory the timing of various life activities in insects differ between females and males. The differences may concern seasonality of flight (Novák 1974) and other activities related to reproduction. Cases where males are active before females (protandry) prevail over the reverse situation (protogyny). This may be a consequence of sexual differences in the developmental times, which may be due to the fact that male gametes are in excess and a male is usually able to inseminate several females. The loss of a male is thus demographically less important than the loss of a female. Therefore males are adapted to withstand the risks associated with waiting and always being prepared for copulation.

Evolution of protandry is explained either in terms of direct selection, or as a consequence of the differences in the body size of the sexes (Wiklund & Solbreck 1982, Wiklund & Forsberg 1991, Wiklund et al. 1991, Nylin et al. 1993). Selection for rapid male development likely to occur in species with discrete generations in which precocious males have a greater probability of copulation than those that emerge later Sexual dimorphism in body size may also result in protandry if larval growth rate is similar in both sexes. The large sex (usually the female) would then take longer to develop. Protandry would then be a consequence of selection favouring maximized body size and fecundity of females. These theories have been tested by Nylin et al. (1993) who have shown an advantage of protandry in a species with discrete generations, but little difference in developmental time that can be related to differences in body size. In fact, the relationships between growth rate, developmental time and final size is mediated by neuroendocrine mechanisms which modify the effect of temperature on the above characters (Sehnal 1991, Gu et al. 1992).

Despite the theoretical developments and an abundance of empirical data there is no review of the relative importance of differences in the length of development in protandry and protogyny. Here the data on the effect of temperature on the development of 97 species of insects for which the developmental times of the males and females were reported separately is reviewed. Although most of the information is for species of economic importance, beneficial or harmful, there is little bias in the data with respect to the factors that might affect the degree of protandry or protogyny: seasonality and sexual size dimorphism. This review includes only those species that develop without entering diapause.

MATERIAL AND METHODS

The data

The information on the effect of constant temperatures on insect development was obtained from the literature. To prevent bias from subjective selection all the data was analysed. The data (Appendix) is for 97 species of insects, 12 Coleoptera, 12 Diptera, 4 Heteroptera, 13 Homoptera, 29 Hymenoptera, 23 Lepidoptera, 3 Orthoptera and 1 Thysanoptera. For some species there was data for several populations.

Lower developmental threshold (LDT, the temperature at which growth ceases) and sum of effective temperatures (SET, the day degrees required for development) were calculated using data for temperatures of 28 °C, and in those species where the LDT>17 °C for temperatures of 30 °C. Thermal characteristics LDT and SET were calculated from a linear regression $1/D = aT + b$, where D is the length of development (days), T is temperature (°C), and a and b are regression coefficients. The $LDT = -b/a$, and $SET = 1/a$. Although linear regression does not describe the development rate/temperature relationship perfectly (cf. Hagstrum & Milliken 1988, Subramanyam & Hagstrum 1993), nevertheless, it provides a sufficiently *precise description for comparing male and female data over a range of ecologically favourable temperatures.*

Classification of the differences

Males and females typically differ in the slope and the intercept of the development rate (1/D) /temperature regression lines. *The temperature at which the regression lines intersect, T_{eq}, is that at which both males and females take the same time to* develop. The range of biologically relevant temperatures considered were LDT=<T=<30 °C. Six types of relationships were distinguished (Fig. 1) which reflect differences in the slopes (a) of the regression lines ($a_{male}>a_{female}$ or $a_{female}>a_{male}$), or the position of T_{eq} with respect to the range of temperatures (T_{eq}<LDT, LDT<T_{eq}<30 °C, T_{eq}>30 °C). These relationships are designated A–F throughout the text: A – Protandry at all temperatures with the difference in the developmental time of the sexes decreasing with increase in temperature. B – protogyny, the difference decreases with temperature. C – protogyny, the difference increases with temperature. D – Protandry, the difference increases with temperature. E – There is a switch from *protandry to protogyny as the temperature increases. F – The switch is from protogyny to protandry.*

As a rule, development is slow and not completed at temperatures near to the lower developmental threshold (T=<LDT+5 °C). Therefore, in developmental types E and F, if T_{eq} is close to the lower developmental threshold (T_{eq}=<LDT+5 °C) protogyny or protandry over the range of temperatures between LDT and T_{eq} has little biological significance. Over the range of temperatures (LDT+5 °C)=<T=<30 °C the development in type E is protogynic and in type F protandric. Effectively protandric or protogynic species are those that are protandric or protogynic over the above range of temperatures, i. e., effectively protandric species are those with developmental types A, D, and F if T_{eq}<LDT+5 °C, and effectively protogynic species *with types B, C, and E if T_{eq}<LDT+5 °C.*

The differences in male and female development times were calculated for 10, 15, 20, 25 and 30 °C, provided these temperatures were 1 °C above the LDT of the sex with the higher threshold. The difference is expressed in days or as a percentage of developmental time of the slow developing sex. Expected standard deviation (SD_e) of development time was calculated as $SD_e = 0.209\,X^{0.730}$ where X is mean development time (Shaffer 1983). Expected coefficients of variation were calculated as $CV = 100(SD_e/X)$.

RESULTS

1. The distribution of development types between stadia and orders

The frequency of developmental types A–F in larvae and pupae differed significantly (Table 1, $\chi^2=22.6$, df=5, $p<0.001$), largely due to the incidence of types D and E. For complete (egg-to-adult) development the frequency of development types did not differ significantly from that for pupae ($\chi^2=11.0$, df=5, N. S.) or larvae ($\chi^2=8.5$, df=5, N. S.). The differences between orders were not significant.

2. Incidence of protandry and protogyny

On the basis of larval development most (64%) species can be classified as protandrous (table 2). Species that showed a switch from protandry to protogyny (or *vice versa*) were relatively frequent (29%), but protogynous species were rare (7%). In contrast for pupae protogynous development was commonest (46%), followed by protandrous development (26%) and a switch from

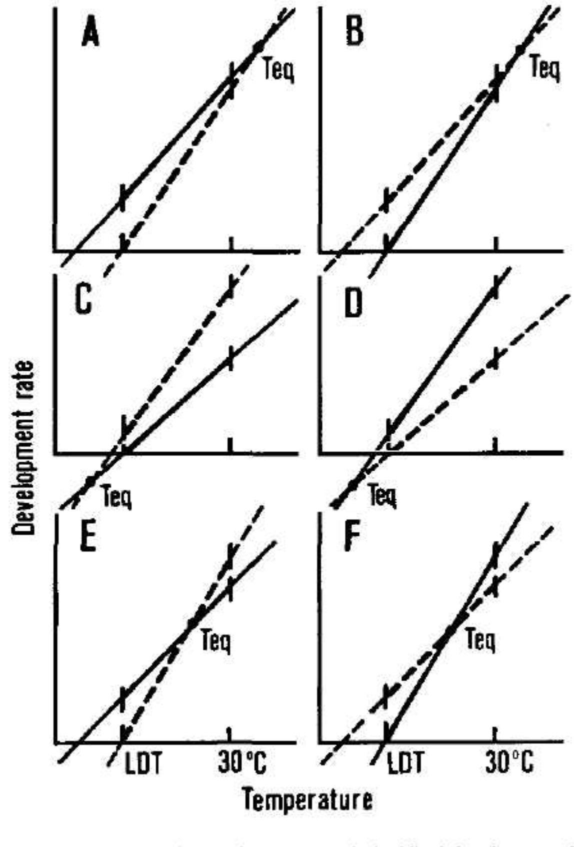

Fig. 1. Relationships between the male (heavy line) and the female (dashed line) developmental rates and temperature: A – The slope of the regression line for male development rate on temperature (a_{male}) is less than that for females (a_{female}); the temperature at which male developmental rate is equal to that for females (T_{eq}) > 30 °C. B – (a_{male}) > (a_{female}); T_{eq} > 30 °C. C – (a_{male}) < (a_{female}); T_{eq} < the upper development thresholds (LDT_u) for males and females. D – (a_{male}) > (a_{female}); $T_{eq} < LDT_u$. E – (a_{male}) > (a_{female}); $LDT_u =< T_{eq} =< 30$ °C. F – (a_{male}) < (a_{female}); $LDT_u =< T_{eq} =< 30$ °C.

Table 1. The distribution of developmental types A–F in larvae, pupae and complete development in several insect orders (see Fig. 1)

Order	Type of sexual difference A	B	C	D	E	F
LARVAE						
Coleoptera	2		1	3		5
Diptera				2	1	2
Heteroptera	1				1	2
Homoptera				2	1	7
Hymenoptera	1			1		2
Lepidoptera	2		1	3	2	9
Orthoptera				1	1	1
Thysanoptera				1		
Sum total	6		2	13	6	28
PUPAE						
Coleoptera	1	1	2		3	3
Diptera			1	3	1	
Hymenoptera	1		1	1	2	3
Lepidoptera	1	1	2		12	4
Sum total	3	2	6	4	18	10
COMPLETE DEVELOPMENT						
Coleoptera	1		1	4	2	2
Diptera		1		3	1	
Heteroptera					2	1
Homoptera	1				1	8
Hymenoptera		1	1	5	5	17
Lepidoptera	1	2	3	1	7	9
Orthoptera						1
Thysanoptera				1		
Sum total	3	4	5	14	18	38

protandry to protogyny (or *vice versa*) (26%). For complete preimaginal development the distribution was similar to that based on larval development, but protandry was less dominant with 43% of the species protandric, 38% showing a switch in development and 18% protogynic. The absence of a difference in the developmental time of males and females was rare. The difference in the frequency of effective protandry, protogyny and switch in developmental types in larvae and pupae was significant (χ^2=23.7, df=2, $p<0.005$), as well as the differences in the frequencies observed in complete and pupal development (χ^2=11.1, df=2, $p<0.005$). The difference in the distribution of developmental types in complete and larval development was not significant (χ^2=5.9, df=2, N. S.).

3. Effect of temperature on the incidence of protandry

With increase in temperature there was an increase in the proportion of species showing protandry, in their larval and complete development (Fig. 2). The ratio of species showing protandry and protogyny differed from 1:1 only at temperatures of 20 °C. The increase in the incidence of protandry with increase in temperature was due to the distribution of T_{eq} for those species that showed a switch between protandry and in their development. For pupae, the proportion of species that showed protandric development varied little and the ratio of protandry to protogyny did not differ significantly from 1:1.

Table 2. Proportion of populations that showed protandry, protogyny, a switch in development and no difference in developmental time between the sexes

Development	Larva	Pupa	Total
Protandry	35 (63.6)	12 (26.1)	36 (43.4)
Protogyny	4 (7.3)	21 (45.7)	15 (18.1)
Switch	16 (29.1)	12 (26.1)	31 (37.3)
No difference	0 (0.0)	1 (2.2)	1 (1.2)

The differences in the developmental time of the sexes decreased with increase in temperature (Table 3). For larvae at temperatures above 20 °C the difference in development time in protandric species was approximately twice as long as in protogynic species. The same was true for complete development at 25 and 30 °C. However, the differences were not statistically significant because the data was variable.

4. The relative importance of sexual differences in developmental time

The average relative difference in male and female developmental time (expressed as a percentage of the developmental time of the slower growing sex) were similar (Table 3). The scatter was large and the distribution of values was right skewed. Typically, most of the differences were less than 6%. The importance of these differences, however, may be small compared to the large scatter in the individual developmental times. Average expected coefficients of variation of developmental time calculated for larvae and complete development (in males) were 8.3±1.6% and 7.9±1.3% at 20 °C, and 9.4±1.6% and 9.0±1.3% at 25 °C. Comparison with the distribution of coefficients of variation of individual developmental times for several randomly selected species (Fig. 3) showed that a large proportion of the variation in the differences associated with sex was smaller than that caused by various intrinsic or extrinsic factors. Only in a small proportion of differences due to sex was the difference large enough to be significant because of the remarkable individual variation in developmental time.

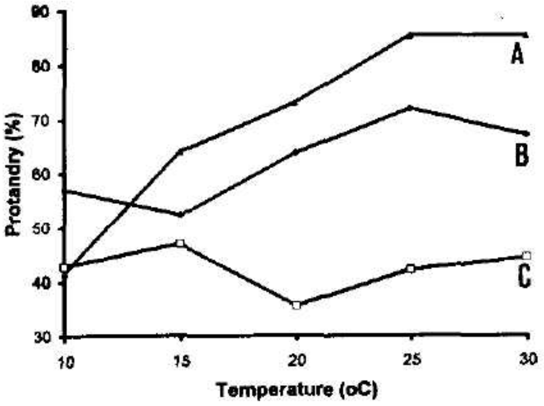

Fig. 2. The proportion of populations that show protandry over a range of temperatures, in larval (L), pupal (P), and complete development (T).

Table 3. The differences in development time in calendar days and expressed as the percentage of the developmental time of the sex with the longer development (mean ± SD and the range of variation in brackets), and the number of species included in the analysis at each temperature (N)

	Protandric development			Protogynic development		
Temperature (°C)	N	Days	Percent	N	Days	Percent
LARVAL DEVELOPMENT						
10	5	5.9±3.7 (1.7–9.8)	9.2±10.5 (1.4–27.2)	7	18.3±22.3 (0.7–63.1)	11.7±12.0 (0.3–35.9)
15	25	11.8±25.5 (0.2–122.2)	11.0±10.9 (0.6–48.6)	14	11.3±18.9 (0.0–57.8)	9.3±11.5 (0.1–35.3)
20	38	8.2±22.9 (0.0–118.7)	9.1±9.6 (0.0–47.9)	14	4.1±6.7 (0.2–24.7)	5.4±7.2 (0.5–23.7)
25	47	3.6±5.5 (0.1–26.3)	9.5±8.2 (0.7–44.9)	8	1.7±2.9 (0.0–8.7)	5.8±9.1 (0.2–27.5)
30	47	2.1±2.6 (0.0–14.8)	9.3±6.3 (0.4–25.7)	8	1.4±2.3 (0.0–7.1)	6.4±10.1 (0.3–30.6)
PUPAL DEVELOPMENT						
10	3	5.7±4.4 (1.0–9.7)	12.3±15.6 (1.9–30.2)	4	13.8±22.0 (0.7–46.7)	14.1±16.6 (1.5–38.5)
15	16	3.0±2.7 (0.4–10.0)	10.4±7.3 (1.6–25.3)	18	3.8±4.4 (0.2–9.2)	9.8±7.9 (0.6–31.1)
20	16	1.5±1.3 (0.2–4.6)	10.1±8.6 (2.7–30.6)	29	1.4±1.5 (0.0–7.2)	8.1±6.8 (0.1–26.7)
25	19	0.8±0.9 (0.0–3.0)	8.7±8.4 (0.3–32.8)	26	0.8±1.0 (0.0–5.1)	8.6±7.7 (0.2–33.8)
30	20	0.6±0.7 (0.1–2.2)	8.5±9.0 (0.9–36.5)	25	0.6±0.8 (0.1–3.9)	9.2±8.4 (1.0–37.5)
COMPLETE DEVELOPMENT						
10	12	23.3±24.8 (2.7–88.0)	12.9±11.2 (1.2–38.6)	9	32.0±34.6 (2.0–91.3)	16.9±13.0 (1.7–45.7)
15	32	8.5±16.9 (1.5–86.7)	7.5±7.1 (0.7–34.6)	29	11.3±15.2 (0.4–65.1)	9.9±10.0 (1.1–37.9)
20	51	5.1±16.5 (0.0–113.4)	6.0±6.2 (0.0–37.7)	29	10.1±34.2 (0.0–183.7)	7.8±13.1 (0.1–60.2)
25	59	2.4±3.8 (0.0–18.2)	6.3±4.7 (0.1–19.0)	23	1.9±3.7 (0.0–16.4)	5.0±7.7 (0.1–32.8)
30	55	1.8±2.3 (0.1–14.3)	7.3±4.6 (0.5–18.8)	27	0.9±1.5 (0.0–6.1)	4.0±6.5 (0.0–32.1)

DISCUSSION

Comparison of the data on the effects of temperature on insect development obtained from the literature is difficult because the authors used different methods. The main sources of error in estimating LDT and SET are the different rearing techniques used and different time intervals at which the development stages were checked. The difference due to sex is less subject to error than comparison between populations since both sexes are usually reared under identical conditions and monitored together. Thus the errors in estimating LDT and SET for males and females are similar and a comparison of the variation due to sex based on the literature is more reliable than a comparison of variation between populations and species. Nevertheless, there are few well documented studies of the effect of temperature on sexual differences in developmental time. There is little data on embryogenesis (e. g. Sedlacek et al. 1990) although differences between the sexes do exist (Sivinski & Calkins 1990). The data for larval and pupal stages and complete development is available only for a few tens of species, whose distribution across the orders is uneven. This is probably related to the ease with which the sex of living individuals may be determined in different groups.

There is a high frequency of protandry in larvae and low freqency in pupae. Larval protandry may have three causes, all of which need further study: (1) greater initial size of male larvae (i. e. males are larger at birth than females), (2) males have a higher growth rate and (3) males terminate their larval development at a smaller size. There is little data on sex related differences in egg size and larval growth rate. Differences in the weight at pupation (or adult ecdysis) of the sexes are well documented. However, larval-pupal or larval-adult moulting is determined several days before ecdysis, by attaining a „critical size“ which is, as a rule, much smaller than the size at termination of feeding (Nijhout & Williams 1974, Honěk 1987, Ochieng-Odero 1990). There is information on the difference between the sexes in the critical size for pupation. Pupal or adult weight is largely determined in the period after attaining the critical size, by nutritional

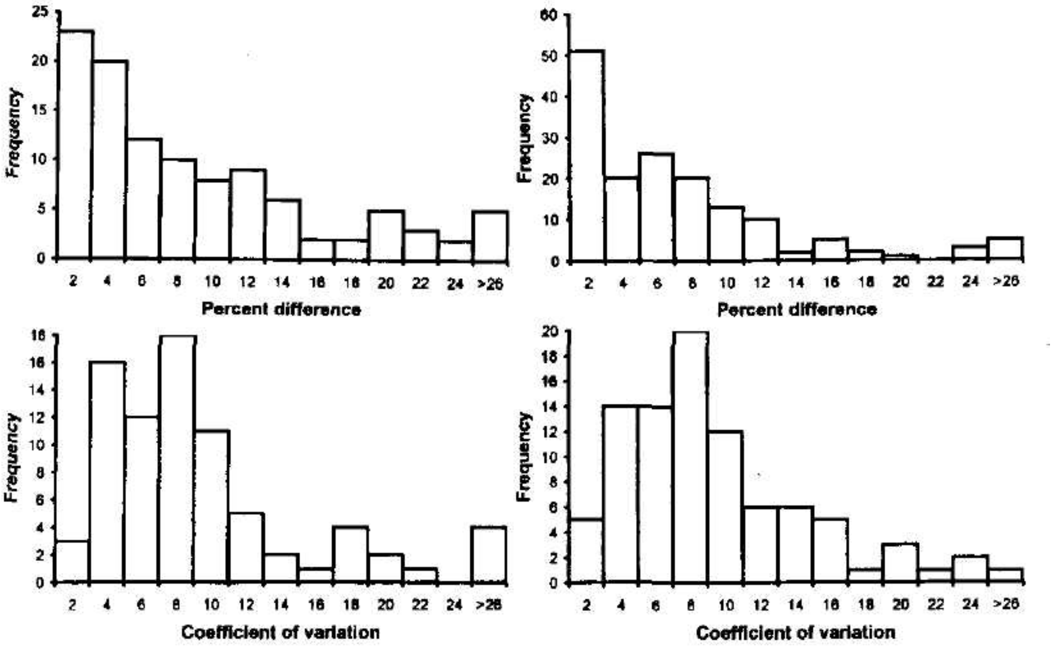

Fig. 3. Above: The distribution of the relative differences in male and female developmental times expressed as percentage of the sex with the longer development time for larvae (left) and complete development (right) at temperatures 20 and 25 °C. Below: The distribution of the coefficients of variation in individual developmental times at temperatures between 18 and 27 °C in several insect species, for larvae (left) and complete development (right). Data from Akey & Kimball 1989, Andrewartha 1936, Bastian & Hart 1991, Begemann 1980, Calvin et al. 1991, Chauvin & Gueguen 1978, DeClercq & Degheele 1992, Etman et al. 1988, Gabriel & Obrycki 1990, Golden & Meinecke 1991, Hoffman et al. 1991, Jacob 1988, James 1992, James & Warren 1991, Michels & Bateman 1986, Michels & Behle 1991, Miller 1992, Miller & Paustian 1992, Neal & Douglass 1990, Ng et al. 1993, Noda 1989, Nylin 1992, Pitcairn et al. 1991, Portillo & Pitre 1992, Powell & Bellows 1992a,b, Rao et al. 1989, Rechav & Orion 1975, Rodriguez-del-Bosque et al. 1989, Rueda et al. 1990, Ryoo & Cho 1988, Sequeira & Mackauer 1992.

factors. Therefore, pupal size is variable and the differences due to temperature and food availability are often not reflected in similar differences in the developmental time (Mukerji & Gupy 1970, van Dijk 1994).

A switch in development from protogyny to protandry or *vice versa* at intermediate temperatures (29% of cases occur during larval development) occurs frequently. This indicates that in many species „protandric“ or „protogynic“ development is not fixed. In some cases at least, the median position of T_{eq} may be an experimental artefact caused by small differences in male and female rate of development over the range of ecologically favourable temperatures.

Pupal protogyny might indicate a higher rate of metamorphosis in female than in male pupae, presumably paralleled by different metabolic rates. In some cases pupal protogyny compensates for larval protandry (Gu et al. 1992). As a result, the difference between the sexes for complete pre-imaginal development are small and parallel the pattern of larval differences. Thus the degree of protandry shown by adults may be small in most cases. This review reveals that the average difference between the sexes is often smaller than the variation in individual developmental times. However, a precise quantification of both sources of variation, using published data, is difficult. The differences in the range of individual variation are huge. This appears to be due more to the way the data were collected than to the taxonomy or ecology of the particular insect. There is need for a study that compares the effect of both sources of variation using a uniform method. Even the present data, however, cast doubt on the adaptive significance of much of the sex-related variation in developmental time.

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APPENDIX

Species included and their basic characteristics, development type (DT), lower development threshold for males (MLDT) and females (FLDT), sum of effective temperatures for males (MSET) and females (FSET), and temperature of equal development length of males and females (T_{eq})

Species	Order[a]	DT[b]	MLDT	FLDT	MSET	FSET	T_{eq}	Reference
TOTAL DEVELOPMENT								
Anthonomus grandis Boehman	Col	C	11.9	11.9	276.9	273.8	11.9	Fye et al. 1969
Anthonomus grandis thurberiae LeConte	Col	E	10.9	11.1	301.8	294.2	18.8	Fye et al. 1969
Dermestes lardarius L.	Col	F	9.8	9.6	717.2	759.9	13.2	Coombs 1978
Trogoderma anthrenoides (Sharp)	Col	B	18.4	15.5	488.3	546.8	42.6	Burgess & Cammell 1964
Trogoderma glabrum (Herbst)	Col	D	10.2	10.8	910.8	995.3	3.7	Archer & Strong 1975
Trogoderma granarium afrum Priesner	Col	D	19.7	20.0	377.3	389.5	10.4	Badawi 1973
Trogoderma granarium afrum Priesner	Col	A	19.0	20.6	369.3	334.2	35.8	Badawi 1973
Trogoderma irroratum Reitter	Col	D	16.7	17.9	617.8	631.2	–38.6	Badawi 1973
Trogoderma variabile Ballion	Col	F	15.5	12.2	633.7	850.8	25.1	Partida & Strong 1975
Trogoderma versicolor (Creutzer)	Col	D	17.1	17.1	510.2	602.6	17.1	Hadaway 1955
Chromatomyia syngenesiae (Hardy)	Dip	D	8.8	8.8	264.4	267.6	8.8	Cheah 1987
Culex theileri (Theobald)	Dip	N	7.9	7.9	218.5	218.5	7.9	Linde et al. 1991
Culex theileri (Theobald)	Dip	D	8.2	8.6	219.2	223.8	–10.9	Linde et al. 1991
Drosophila melanogaster (Meigen)	Dip	B	11.7	11.4	139.6	141.5	32.6	Zwaan et al. 1968
Leschnaultia adusta (Loew)	Dip	D	8.3	8.6	538.6	566.7	2.5	Jackson et al. 1970
Sturmiopsis inferens Townsend	Dip	E	10.1	10.7	409.2	394.3	26.6	David et al. 1981
Lygus desertus Knight	Het	E	11.9	12.2	304.7	298.2	26.0	Butler 1970b
Nysius vinitor Bergroth	Het	F	15.7	15.5	264.5	271.7	23.0	Kehat & Wyndham 1972
Stephanitis pyroides (Scott)	Het	E	12.7	12.8	359.8	351.2	16.9	Neal & Douglas 1988
Aonidiella aurantii (Mask)	Hom	F	12.5	11.5	336.3	437.6	15.8	Yu & Luck 1988
Cicadulina mbila (Naude)	Hom	A	17.7	18.1	206.3	200.5	31.9	Rose 1973
Cicadulina mbila (Naude)	Hom	E	12.9	13.7	343.6	325.4	28.0	van Rensburg 1982
Cicadulina parazae Ghauri	Hom	F	14.4	12.1	325.1	405.2	23.7	Rose 1973
Cicadulina storeyi Chin	Hom	F	17.7	15.4	200.4	289.6	22.9	Rose 1973
Coccobius fulvus (Compere & Annecke)	Hom	F	11.6	11.5	355.6	374.8	13.5	Ogata 1987
Empoasca fabae (Harris)	Hom	F	8.9	8.3	352.2	396.1	13.7	Sher & Shields 1991
Graminella nigrifrons (Forbes)	Hom	F	13.8	13.2	311.0	349.3	18.7	Sedlacek et al. 1990
Phenacoccus herreni Cox & Williams	Hom	F	15.8	15.4	195.8	207.6	22.4	Herrera et al. 1989
Pseudaulacaspis pentagona (Targioni-Tozzeti)	Hom	F	5.9	4.6	447.3	528.5	13.0	Ball 1980
Anagrus giraulti Crawford	Hym	E	10.2	10.3	195.8	194.6	26.5	Meyerdirk & Moratorio 1987
Anisopteromalus calandrae (Howard)	Hym	D	16.5	16.8	133.8	137.5	5.7	Smith 1992
Aphidius colemani Viereck	Hym	E	4.0	1.5	201.6	235.2	19.0	Steenis 1993
Aphytis mellinus DeBach	Hym	F	13.3	13.4	187.6	187.7	–174.3	Abdelrahman 1974
Brachymeria lasus (Walker)	Hym	F	12.9	12.3	176.0	202.4	15.9	Mao & Kunimi 1994
Bracon mellitor Say	Hym	F	11.0	9.6	205.5	264.4	15.9	Barfield et al. 1977
Chrysocharis parksi Crawford	Hym	F	12.1	11.2	207.8	224.8	23.1	Christie & Parella 1987

continued

Species	Order[a]	DT[b]	MLDT	FLDT	MSET	FSET	T_{eq}	Reference
Diglyphus isaea Walker	Hym	E	11.0	11.1	183.1	181.7	24.1	Cheah 1987
Diglyphus isaea Walker	Hym	F	9.0	8.6	167.3	176.1	16.6	Minkenberg 1989
Diglyphus isaea Walker	Hym	E	7.9	8.8	165.7	154.2	20.9	Minkenberg 1989
Encarsia formosa Foerster	Hym	C	9.7	9.0	386.5	271.5	7.3	Avila & Copland 1988
Encarsia perniciosi (Tower)	Hym	F	8.0	5.2	399.3	520.1	17.3	McClain et al. 1990
Eremocentrus sp.	Hym	E	9.4	10.6	373.1	337.5	22.0	Powell & Bellows 1992b
Eremocentrus sp.	Hym	F	13.2	12.7	240.2	265.4	18.0	Powell & Bellows 1992b
Gonatocerus cincticipitis Sakai	Hym	E	11.0	11.4	169.8	166.2	29.9	Miura 1990
Metaphycus bartletti Annecke & Mynhardt	Hym	B	11.7	11.6	316.5	317.4	46.9	Blumberg & Swirski 1982
Metaphycus swirskii Annecke & Mynhardt	Hym	F	11.5	11.0	254.0	266.6	21.6	Blumberg & Swirski 1982
Microplitis rufipes Kokujev	Hym	D	10.2	10.5	200.7	210.0	3.7	Hutchinson et al. 1986
Patasson lameerei Debauche	Hym	D	5.6	5.6	241.4	269.5	5.6	Leibee et al. 1989
Pimpla instigator (F.)	Hym	F	7.8	7.2	329.7	377.1	12.0	Claret 1978
Telenomus podisi Ashmead	Hym	F	13.9	12.9	138.1	169.1	18.4	Yeargan 1980
Telenomus reynoldsi Gordh & Coker	Hym	F	14.7	14.5	170.0	177.5	19.2	Cave & Gaylor 1988
Telenomus reynoldsi Gordh & Coker	Hym	F	14.3	14.3	158.1	166.3	16.0	Cave & Gaylor 1988
Telenomus reynoldsi Gordh & Coker	Hym	D	14.3	14.3	158.1	166.3	14.3	Cave & Gaylor 1988
Telenomus reynoldsi Gordh & Coker	Hym	D	14.2	14.4	153.9	160.0	9.2	Cave & Gaylor 1988
Trichogramma chilonis Ishii	Hym	F	8.8	8.5	150.7	155.0	19.3	Miura & Kobayashi 1993
Urolepis rufipes Ashmead	Hym	F	16.0	15.9	108.0	117.8	17.1	Smith & Rutz 1986
Urolepis rufipes Ashmead	Hym	F	12.5	11.7	149.7	171.4	17.5	Matthews & Paterson 1989
Urolepis rufipes Ashmead	Hym	F	12.7	11.5	185.6	216.0	20.0	Matthews & Paterson 1989
Ancylis comptana (Froelich)	Lep	F	10.7	10.5	391.3	415.4	13.9	Gabriel & Obrycki 1990
Argyrotaenia velutinana (Walker)	Lep	F	8.2	8.0	610.9	696.5	9.6	Hawthorne et al. 1988
Choristoneura occidentalis Freeman	Lep	D	6.7	6.9	670.3	686.8	−1.4	Reichenbach & Stairs 1984
Crocidosema plebejana (Zeller)	Lep	F	11.2	11.0	369.1	391.4	14.5	Hamilton & Zalucki 1991
Diatraea lineolata (Walker)	Lep	F	11.3	9.8	701.9	802.3	21.8	Rodriguez-del-Bosque et al. 1989
Diatraea saccharalis (F.)	Lep	F	14.1	13.5	431.1	479.5	19.4	King et al. 1975
Heliothis armigera (Hubner)	Lep	C	11.2	11.0	503.6	483.3	6.2	Wu et al. 1980
Heliothis armigera (Hubner)	Lep	B	14.3	13.7	339.2	349.9	33.3	Twine 1978
Lobseia botrana (Denis & Schiffermuller)	Lep	A	7.4	9.3	625.0	588.2	39.7	Gabel 1981
Merophyas divulsana (Walker)	Lep	F	8.5	8.2	448.3	460.1	19.9	Allsopp et al. 1983
Mythimna convecta (Walker)	Lep	E	6.9	7.2	828.7	775.0	11.5	Smith 1984
Pararge aegeria L.	Lep	F	5.5	5.4	576.8	623.8	6.7	Nylin et al. 1993
Pararge aegeria L.	Lep	E	5.2	6.5	524.7	469.2	17.5	Nylin et al. 1993
Pararge aegeria L.	Lep	F	5.7	4.8	546.3	611.5	13.2	Nylin et al. 1993
Pectinophora gossypiella (Saunders)	Lep	E	13.6	13.6	454.5	449.4	13.6	Raina et al. 1973
Plathypena scabra (F.)	Lep	E	8.4	8.6	595.8	547.9	10.9	Hammond et al. 1979
Plutella xylostella (L.)	Lep	E	7.5	7.5	286.0	281.0	7.5	Umeya & Yamada 1973
Plutella xylostella (L.)	Lep	B	9.7	9.5	226.6	228.6	32.4	Umeya & Yamada 1973
Spodoptera frugiperda (Smith)	Lep	F	14.5	12.8	315.0	405.5	20.4	Barfield et al. 1978
Spodoptera littoralis (Boisduval)	Lep	C	11.6	11.4	524.7	484.2	9.0	Baker & Miller 1974
Spodoptera littoralis (Boisduval)	Lep	E	11.4	12.2	283.3	242.5	17.0	Bhatt & Bhattacharya 1976
Spodoptera littoralis (Boisduval)	Lep	E	10.3	10.3	320.2	310.6	10.3	Bhatt & Bhattacharya 1976
Trichoplusia ni (Hubner)	Lep	C	12.6	12.3	332.9	331.6	−64.2	Toba at al. 1973
Eyprepocnemis allacris Serville	Ort	F	16.9	16.1	980.8	1239.4	19.9	Khan & Azziz 1974
Thrips obscuratus (Crawford)	Thy	D	4.2	4.9	218.0	229.5	−9.1	Teulon & Penman 1991
PUPAE								
Diabrotica virgifera virgifera LeConte	Col	F	10.7	10.6	104.7	108.9	13.2	Jackson & Elliott 1988
Trogoderma anthrenoides (Sharp)	Col	N	15.4	15.4	91.0	91.0	15.4	Burgess & Cammell 1964
Trogoderma glabrum (Herbst)	Col	F	18.3	17.9	43.0	45.7	24.7	Archer & Strong 1975
Trogoderma granarium Everts	Col	A	11.6	15.0	70.0	60.0	35.4	Hadaway 1955
Trogoderma granarium afrum Priesner	Col	E	17.6	17.6	53.4	49.6	17.6	Badawi 1973
Trogoderma granarium afrum Priesner	Col	E	17.5	17.9	56.3	49.5	20.8	Badawi 1973
Trogoderma inclusum LeConte	Col	B	17.5	16.7	43.7	45.5	36.9	Strong 1975
Trogoderma irroratum Reitter	Col	C	16.7	16.7	66.7	66.0	16.7	Badawi 1973
Trogoderma somplex Jayna	Col	E	17.1	17.2	61.5	57.5	18.6	Strong & Mead 1975

Trogoderma variabile Ballion	Col	C	17.3	17.0	48.3	47.6	–3.4	Partida & Strong 1975
Trogoderma versicolor (Creutzer)	Col	F	15.0	13.5	60.0	76.6	20.4	Hadaway 1955
Culicoides mississippiensis Hoffman	Dip	E	9.4	10.2	52.1	47.5	18.5	Davis et al. 1983
Culicoides mississippiensis Hoffman	Dip	D	9.0	9.1	56.6	58.0	5.0	Davis et al. 1983
Haematobia irritans exigue deMeijere	Dip	C	11.1	11.1	108.5	98.4	11.1	Cook & Spain 1981
Leschnaultia adusta (Loew)	Dip	D	8.9	9.0	333.0	363.0	7.8	Jackson et al. 1970
Lixophaga diatraeae (Townsend)	Dip	D	10.8	10.8	124.2	166.3	10.8	King & Martin 1975
Apantheles fumiferanae (Viereck)	Hym	F	10.0	12.9	115.5	61.7	16.2	Lysyk & Nealis 1988
Brachymeria lasus (Walker)	Hym	F	13.3	12.8	73.6	86.3	16.2	Mao & Kunimi 1994
Cotesia urabae Austin & Allen	Hym	F	10.3	10.0	74.5	83.8	12.7	Gould & Elkinton 1990
Cotesia urabae Austin & Allen	Hym	C	9.3	9.7	89.0	89.0		Allen & Keller 1991
Diglyphus isaea (Walker)	Hym	F	8.0	7.6	87.1	96.4	11.7	Minkenberg 1989
Diglyphus isaea (Walker)	Hym	A	5.7	7.1	96.3	93.0	46.6	Minkenberg 1989
Glypta fumiferanae Viereck	Hym	E	7.2	9.3	183.1	150.1	18.9	Lysyk & Nealis 1988
Megachile pacifica Panzer	Hym	F	18.4	18.1	89.1	108.7	19.8	Tasei & Masure 1978
Microplitis rufiventris Kokujev	Hym	D	10.3	11.2	83.5	84.3	–83.6	Hutchinson et al. 1986
Argyrotaenia velutinana (Walker)	Lep	E	9.5	10.1	129.5	122.0	19.9	Hawthorne et al. 1988
Attacus ricini (Boisduval)	Lep	F	10.4	10.3	231.6	251.2	11.6	Gomaa 1973
Attacus ricini (Boisduval)	Lep	F	9.1	8.5	259.5	270.0	23.9	Gomaa 1973
Autographa biloba (Stephens)	Lep	E	12.2	12.3	121.5	116.5	14.6	Beach & Todd 1985
Choristoneura pinus pinus Freeman	Lep	F	13.2	10.6	57.4	104.9	16.5	Lysyk & Nealis 1988
Diatraea lineolata (Walker)	Lep	F	12.4	10.7	151.3	172.5	24.5	Rodriguez-del-Bosque et al. 1989
Diatraea saccharalis (F.)	Lep	F	15.8	15.5	83.1	85.6	25.8	King et al. 1975
Heliothis armigera (Hubner)	Lep	E	12.8	12.8	191.4	171.1	12.8	Wu et al. 1980
Lobesia botrana (Dennis & Schiffermuller)	Lep	A	7.1	9.1	162.1	151.5	37.7	Gabel 1981
Merophyas divulsana (Walker)	Lep	E	7.8	7.9	113.0	98.4	8.8	Allsopp et al. 1983
Mythimna convecta (Walker)	Lep	E	8.1	8.3	243.7	228.9	11.4	Smith 1984
Pectinophora gossypiella (Saunders)	Lep	E	11.6	12.1	143.5	131.6	17.6	Raina et al. 1977
Plathypena scabra (F.)	Lep	E	10.2	10.8	146.5	124.9	14.3	Hammond et al. 1979
Platynota idaeusalis (Walker)	Lep	B	8.9	8.2	133.6	134.5	112.8	Rock 1985
Platynota idaeusalis (Walker)	Lep	C	10.3	9.8	118.2	112.6	–0.3	Mawby & Rock 1986
Plutella xylostella (L.)	Lep	E	8.4	8.5	74.9	69.2	9.7	Umeya & Yamada 1973
Plutella xylostella (L.)	Lep	E	8.7	8.9	68.5	59.1	10.2	Umeya & Yamada 1973
Spodoptera littoralis (Boisduval)	Lep	E	11.8	12.8	222.3	143.1	14.6	Baker & Miller 1974
Trichoplusia orichalcea (F.)	Lep	E	10.2	10.6	122.6	110.7	14.3	Cabello 1988
Trichoplusia orichalcea (F.)	Lep	E	11.6	11.8	125.6	108.0	13.0	Cabello 1988
Uraba lugens Walker	Lep	C	9.3	9.0	228.0	218.0	2.5	Allen & Keller 1991
LARVAE								
Ceutorrhynchidius horridus (Panzer)	Col	C	0.9	0.4	1362.1	1359.1	–226.1	Kok et al.1975
Diabrotica virgifera virgifera LeConte	Col	F	10.7	9.9	236.0	277.6	15.2	Jackson & Elliott 1988
Trogoderma anthrenoides (Sharp)	Col	F	18.8	18.7	333.9	395.0	19.3	Burgess & Cammell 1964
Trogoderma glabrum (Herbst)	Col	D	8.2	9.5	768.8	837.6	–6.3	Archer & Strong 1975
Trogoderma granarium Everts	Col	F	14.3	12.8	350.6	450.6	19.6	Hadaway 1955
Trogoderma granarium afrum Priesner	Col	D	20.3	20.6	253.6	272.0	16.2	Badawi 1973
Trogoderma granarium afrum Priesner	Col	A	17.3	21.1	248.3	228.3	64.5	Badawi 1973
Trogoderma irroratum Reitter	Col	D	16.3	18.0	477.5	495.6	–28.5	Badawi 1973
Trogoderma variabile Ballion	Col	F	15.3	11.1	489.4	707.3	24.7	Partida & Strong 1975
Trogoderma variabile Ballion	Col	A	17.3	19.1	372.4	358.5	65.5	Elbert 1974
Trogoderma versicolor (Creutzer)	Col	F	17.9	17.4	370.1	452.2	20.2	Hadaway 1955
Aedes nigromaculatus (Ludlow)	Dip	E	17.0	17.1	48.5	47.8	23.9	Brust 1967
Aedes togoi (Theobald)	Dip	D	11.4	11.4	121.9	133.5	11.4	McGinnis & Brust 1983
Aedes vexans (Meigen)	Dip	D	15.9	16.1	49.9	52.6	12.2	Brust 1967
Culiseta inornata (Williston)	Dip	F	9.4	8.2	146.4	208.6	12.2	Brust 1967
Lixophaga diatreae (Townsend)	Dip	F	11.5	10.8	105.7	124.2	15.5	King & Martin 1975
Lygus desertus Knight	Het	E	12.2	12.6	185.6	174.3	18.8	Butler 1970
Nysius vinitor Bergroth	Het	F	16.0	15.8	197.2	203.9	21.9	Kehat & Wyndham 1972
Stephanitis pyroides (Scott)	Het	A	12.6	13.0	183.0	179.5	33.5	Neal & Douglas 1988
Spanagonias albofasciatus (Reuter)	Het	F	15.0	14.8	145.3	149.8	21.5	Butler 1970a
Empoasca fabae (Harris)	Hom	F	8.8	7.7	210.6	258.6	13.6	Sher & Shields 1991
Graniella nigrifrons (Forbes)	Hom	F	13.7	12.6	212.9	254.4	19.3	Sedlacek et al. 1990
Laodelphax striatella (Fallén)	Hom	F	12.6	12.1	165.3	185.4	16.7	Noda 1989
Laodelphax striatella (Fallén)	Hom	D	11.6	11.6	184.7	192.2	11.6	Noda 1989
Laodelphax striatella (Fallén)	Hom	F	12.0	11.7	168.9	183.7	15.4	Noda 1989

continued

Species	Order[a]	DT[b]	MLDT	FLDT	MSET	FSET	T_{eq}	Reference
Lepidoaspis beckii Newman	Hom	E	11.5	13.4	426.7	265.7	21.7	Hafez & Salama 1969
Nilaparvata lugens (Stål)	Hom	F	11.8	11.7	179.3	188.1	13.8	Noda 1989
Phenacoccus herreni Cox & Williams	Hom	F	16.1	15.6	127.7	139.2	21.7	Herrera et al. 1989
Pseudaulacaspis pentagona (Targioni-Tozzeti)	Hom	F	4.2	2.3	419.6	515.6	12.5	Ball 1980
Sogatella furcifera (Horvath)	Hom	D	11.7	11.8	158.5	167.3	9.9	Noda 1989
Apantheles fumiferanae (Viereck)	Hym	F	9.8	9.2	254.8	336.9	11.7	Lysyk & Nealis 1988
Cotesia urabae Austin & Allen	Hym	D	6.5	6.5	317.0	349.0	6.5	Allen & Keller 1991
Glypta fumiferanae Viereck	Hym	A	8.9	9.1	383.3	381.8	60.0	Lysyk & Nealis 1988
Microplitis rufiventris Kokujev	Hym	F	10.0	9.5	117.0	128.6	15.0	Hutchinson et al. 1986
Argyrotaenia velutinana (Walker)	Lep	F	7.4	6.3	360.2	471.4	11.0	Hawthorne et al. 1988
Autographa biloba (Stephens)	Lep	F	11.6	10.6	211.8	231.2	22.5	Beach & Todd 1985
Choristoneura occidentalis Freeman	Lep	F	8.6	8.4	281.8	321.0	10.0	Reichenbach & Stairs 1984
Diatraea lineolata (Walker)	Lep	F	10.8	8.7	472.2	559.8	22.1	Rodriguez-del-Bosque et al. 1989
Diatraea saccharalis (F.)	Lep	F	13.3	12.2	278.4	322.5	20.2	King et al. 1975
Lobesia Botrana (Dennis & Schiffermuller)	Lep	A	7.3	9.4	384.6	362.3	43.5	Gabel 1981
Merophyas divulsana (Walker)	Lep	F	8.6	8.1	250.7	277.9	13.2	Allsopp et al. 1983
Mythimna convecta (Walker)	Lep	E	5.8	6.2	502.9	461.4	10.7	Smith 1984
Pectinophora gossypiella (Saunders)	Lep	F	12.0	11.9	293.0	297.3	18.8	Raina et al. 1977
Platynota idaeusalis (Walker)	Lep	D	9.9	10.0	325.9	339.5	7.5	Rock 1985
Platynota idaeusalis (Walker)	Lep	D	9.4	9.5	328.0	334.0	3.9	Mawby & Rock 1986
Plathypena scabra (F.)	Lep	C	6.2	6.2	401.5	376.2	6.2	Hammond et al. 1979
Plutella xylostella (L.)	Lep	F	10.0	9.7	158.7	169.3	14.5	Umeya & Yamada 1973
Plutella xylostella (L.)	Lep	D	6.8	6.9	217.5	219.0	−7.7	Umeya & Yamada 1973
Trichoplusia orichalcea (F.)	Lep	F	11.3	11.0	194.1	206.7	15.9	Cabello 1988
Trichoplusia orichalcea (F.)	Lep	E	8.0	8.1	269.0	267.0	21.5	Cabello 1988
Uraba lugens Walker	Lep	A	11.5	13.2	453.0	453.0		Allen & Keller 1991
Eyprepocnemis alacris Serville	Ort	F	17.6	16.6	684.5	937.7	20.3	Khan & Aziz 1974
Monistra discrepans (Walker)	Ort	D	16.7	17.7	578.0	590.2	−30.7	Allsopp 1972
Taeniopoda eques (Burmeister)	Ort	E	17.8	17.9	434.6	426.6	23.2	Whitman 1986
Thrips oscuratus (Crawford)	Thy	D	4.2	5.5	151.7	161.6	−15.7	Teulon & Penman 1991

[a] Col – Coleoptera, Dip – Diptera, Het – Heteroptera, Hom – Homoptera, Hym – Hymenoptera, Lep – Lepidoptera, Ort – Orthoptera, Thy – Thysanoptera

[b] Development types A–F – see explanation in Fig. 1, N – no difference

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A review of Chinese *Aphodius* species. Part 4: subgenera *Pseudacrossus* and *Qingaphodius* sbg. n. (Coleoptera: Scarabaeidae)

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Abstract. Chinese species of *Aphodius* Illiger, 1798 subgenus *Pseudacrossus* Reitter, 1892 are reviewed. Two new species from the Qinghai province, *A.* (*P.*) *kalabi* sp. n. and *A.* (*P.*) *qinghaiensis* sp. n., both closely related to *A.* (*P.*) *przewalskyi* Reitter, 1887, are described. *A.* (*P.*) *subsericeus* Ballion, 1878 comb. n. is transferred from the subgenus *Amidorus* Mulsant et Rey, 1869. Lectotypes and/or paralectotypes for *A.* (*P.*) *grombczewskyi* D. Koshantschikov, 1891, *A.* (*P.*) *nasutus* Reitter, 1887, *A.* (*P.*) *przewalskyi* Reitter, 1887, *Aphodius consors* Reitter, 1892, *A. kelleri* W. Koshantschikov, 1911, *A. mehelyi* Csiki in Zichy, 1901, and *A. roschlapili* Csiki in Zichy, 1901 are designated (last four taxa as synonyms to *A.* (*P.*) *nasutus*). *A.* (*P.*) *grombczewskyi* is recorded from China (Xinjiang) for the first time. A new subgenus from the Qinghai province, *Aphodius* (*Qingaphodius* sbg. n.) for *A.* (*Q.*) *nikodymi* sp. n. and *A.* (*Q.*) *ochotonarum* sp. n. is proposed. Both new species are tied with small mammals, the former with *Marmota himalayana* (Hodgson, 1841), the latter with *Ochotona* sp. Chinese *Pseudacrossus* and *Qingaphodius* sbg. n. species are keyed, their epipharyngi and male genitalia are figured.

Taxonomy, new subgenus, new species, new combination, distribution, Coleoptera, Scarabaeidae, *Aphodius*, *Amidorus*, *Pseudacrossus*, *Qingaphodius* sbg. n., Palaearctic region

INTRODUCTION

The present part of review of Chinese *Aphodius* Illiger, 1798 species is dealing with the subgenus *Pseudacrossus* and with a new subgenus, *Qingaphodius* sbg. n., related to *Pseudacrossus*. The subgenus *Pseudacrossus* was erected by Reitter in 1892 with a type species *Aphodius* (*Pseudacrossus*) *grombczewskyi*. According to recent world catalogue (Dellacasa 1988) the subgenus comprised 29 species. Nearly all so far known species (28) are confined to the Palaearctic region (including the transitional zone of the Himalayas) and one is described from the Nearctic region. But the subgenus is in my opinion not homogenous. Many species probably belong to other subgenera. Therefore a thorough revision of the majority of species listed in Dellacasa (1988) is badly needed. Six species including two new species described in this paper, are currently known from China. In Dellacasa (1988) there are listed as *Pseudacrossus* species also *Aphodius absconditus* Balthasar, 1932 and *A. juxtus* Petrovitz, 1972, both described from China. I have an opportunity to study the type material of both the species belonging in my opinion to the subgenus *Bodilus* Mulsant et Rey, 1869. *Aphodius peculator* Balthasar, 1971, also listed in Dellacasa (1988) as a *Pseudacrossus* representative and possibly inhabiting China, was transferred by Stebnicka (1989) to the subgenus *Koshantschikovius* A. Schmidt, 1913. A new subgenus, *Qingaphodius* sbg. n., is proposed for the two species described here showing an extraordinary form of sexual dimorphism.

MATERIAL AND METHODS

Mouthparts of three specimens, if available of each species under study, were dissected for examination of epipharyngeal structures. The dissected mouthparts were mounted in the Liquide de Swann on permanent slides and examined with stereoscopic microscope Meopta. All permanent slides are deposited in DKCP. Morphological terminology concerning epipharyngeal structures was adopted from Dellacasa (1983).

The following codes (after Arnett et al. 1993) identify the collections housing the material examined:
BZCL – Czech Republic, Lovosice, Bohdan Zvarič collection;
DEIC – Germany, Eberswalde-Finow, Deutsches Entomologisches Institut (L. Behne);
DKCP – Czech Republic, Praha, David Král collection;
JRCP – Czech Republic, Poděbrady, Jiří Rejsek collection;
HNHM – Hungary, Budapest, Hungarian Natural History Museum (O. Merkl, G. Szél);
MNCP – Czech Republic, Praha, Milan Nikodým collection;
MHNG – Switzerland, Genève, Muséum d'Histoire naturelle (I. Löbl);
MNHN – France, Paris, Muséum national d'Histoire naturelle (Y. Cambefort);
NHMB – Switzerland, Basel, Naturhistorisches Museum (M. Brancucci);
MRCD – Czech Republic, Dobřichovice, Miloslav Rakovič collection;
NMPC – Czech Republic, Praha, National Museum (Natural History) (J. Jelínek);
PBCV – France, Verrières le Buisson, Patrice Bordat collection;
RCCP – Czech Republic, Praha, Radek Červenka collection;
SJCP – Czech Republic, Praha, Stanley Jakl collection;
ZMAS – Russia, St. Petersburg, Zoological Museum, Academy of Sciences (B. M. Kataev, M. G. Volkovich);
ZMHB – Germany, Berlin, Museum für Naturkunde der Humboldt Universtität (F. Hieke, M. Uhlig).

Specimens of the newly described species are provided with one red printed label: "[Name of a taxon] sp. n., HOLOTYPUS, ALLOTYPUS or PARATYPUS with No, ♂ or ♀, David Král det. 1997". In the case of lectotype and/or paralectotype designation, each specimen bears a red printed label: "[Name of a taxon], LECTOTYPUS or PARALECTOTYPUS with No, ♂ or ♀, David Král design. 1997". Exact label data are cited for the material, separate labels are indicated by slashes (/). Author's remarks and complementations are found in square brackets; [p] – preceding data within quotation are printed; [h] – the same but handwritten, [*] – according to personal communication by O. Merkl (HNHM), these red handwritten labels were not written by Reitter but later by a curator of Budapest museum (Kaszab or Székessy); MS – manuscript, HT – holotype, AT – allotype, PT – paratype; x/y – number of males / number of females.

SYSTEMATIC PART

***Aphodius* (*Pseudacrossus*) *grombczewskyi* D. Koshantschikov, 1891**

(Figs 1, 13, 14)

Aphodius (*Amidorus*) *Grombczewskyi* D. Koshantschikov, 1891: 439.
Aphodius (*Pseudacrossus*) *Grombczewskyi*: Reitter, 1892: 218–219.
Aphodius (*Pseudacrossus*) *grombczewskyi*: Nikritin, 1974: 466; G. Dellacasa, 1983: 393, 394–395, figs 919–922; Nikolaev, 1987: 102, 108, 119; M. Dellacasa, 1988: 136, 395.
Aphodius (*Agolius*) *przewalskii* subsp. *grombczewskii*: W. Koshantschikov, 1911: 205–208.
Aphodius (*Pseudagolius*) *przewalskyi* var. *grombczewskyi*: Schmidt, 1913: 150; 1922: 235.
Aphodius (*Pseudacrossus*) *przewalskyi grombczewskyi*: Nikritin, 1973: 615.
Aphodius (*Pseudacrossus*) *Przewalskyi* var. *Daraignezi* Clérmont, 1907: 170.
Aphodius (*Pseudagolius*) *przewalskyi* var. *daraignezi*: Schmidt, 1913: 150; 1922: 235.
Aphodius (*Pseudacrossus*) *przewalskyi* ab. *daraignezi*: Balthasar, 1964: 309.
Aphodius (*Pseudacrossus*) *grombczewskyi* ab. *daraignezi*: G. Dellacasa, 1983: 395; M. Dellacasa, 1988: 118, 395.

TYPE LOCALITY. Alai-Gebirge (D. Koshantschikov 1891).

TYPE MATERIAL EXAMINED. Lectotype and 10 paralectotypes by present designation: Lectotype (male) and paralectotypes No 1 (male) and Nos 2–10 (females): "Turkestan Alai [mts] [h] / *Aphodius Grombczevskii Kosh.* [probably *D. Koshantschikov's* MS]", all in ZMAS; paralectotype No 11 (male): "Alai Geb. [mts] [h] / Syntypus [p, red label] / Aphodius Grombczewskyi mihi [D. Koshantschikov's MS]", in DEIC.

Additional material examined. **China, Xinjiang**: Dsungaria, Borochoro-Gb. [mts], 6.05, coll. Hauser, 1 spec. in HNHM; Chan-Tengri, mont. merid, 4 spec. in ZHMB; Tien-chan, valée de Youldouz et du Koksou, Dr. L. Vaillant 1909, Aout, 2 spec. in MNHN; China, 87°11 E, 43°16 N, Xinjiang Uygur reg., Houxia, 2500 m, 17.–21.VII.1991, 6 spec. in DKCP; China, Xinjiang, ca 2800 m, N slope of Tian Shan mts., road Kuqa – Bayanbulak, 50 km SW Bayanbulak, 11–13/5.1993, 3 spec. in DKCP; China, Xinjiang, 2000–2500 m, NE slope of Tian Shan mts., road Urumqi – Houxia, ca 60 km SW Urumqi, 15–17/5.1993, 7 spec. in DKCP; China – prov. Xin Yang [=Xinjiang], Ťan-Šan, Bayangol, 2100 m, 21.VII.1994, 4 spec. in DKCP. **Kazakhstan**: Turkestan, Narynkol, Almásy, 1906, 13 spec. in HNHM and 5 spec. in MHNG; Kazakhstan, Alma Ata, 10.8.1942, lg. D. Zay [label written in Cyrillic script], 1 spec. in HNHM, 4 spec. in ZHMB; Alatau [mts], Wernoje [=Alma-Ata], 4 spec. in HNHM; Aulie Ata [=Dzhambul], Syrdarja, 5 spec. in MHNG; Kara-kja, Semirjetschensk, 1 spec. in MHNG; Semirjetschensk, Kamenaja-ret., coll. Winkler, 1 spec. in MHNG; Semirjetschensk, Almatinka Tal, 1 spec. in MHNG; Semirjetschensk, Karkara, 9 spec. in MHNG; Tschapkandjol, Semirjetschensk, 1 spec. in MHNG; Thian-S., Tekesthal, 1 spec. in HNHM; Turkestan, Aulie Ata [=Dzhambul], 5 spec. in HNHM; Vernoje [=Alma-Ata], Stauding., 1 spec. in DEIC; Wernyi [=Alma-Ata], Turkest., 1 spec. in MHNG, 3 spec. in HNHM; Wernoje [=Alma-Ata], coll. Hauser, 3 spec. in MHNG; Kazakhistan, Terskej Alatau, 6. 1958, 1 spec. in DEIC; Medeo-Kazachstan, Zaalijský Ala Tau [mts], 1800–2400 m, 30.7.87, Z. Mašek lgt., 1 spec. in DKCP; USSR, Kazachstan, Alma Ata env., Levyj Talgar vall., 2000–2500 m, 16.6.89, 2 spec. in RCCP; SU, Kazachstan, Panfilov [=Dzharkent] , Dzhungarskyi Ala Tau [mts], 20.–26.6.91, 2500 m, 44° 30'[N] 79° 30" [E], M. Kafka lgt., 3 spec. in DKCP, 3 spec. in RCCP; S.O. Kasachstan, Orta-Tau Geb.-Kette, Orta Karagajlly Schl., 2000–2400 m, 6.–10.06.91, 1 spec. in DKCP, 12 spec. NHMB; S.-O. Kasachstan, A-Ata gross-Schlucht, 2500–3100 m, 26–30.06.91, Andreewa lgt., 2 spec. in NHMB **Kyrgyzstan**: Turkestan, Almásy 1906, Naryn, 12 spec. in HNHM; Central Tjan-Shan, Naryngebiet Fluss, tal Kara-Kuldschur, 3100 m, VII–IX, 1934, 3 spec. in MHNG; Karagaitau, 1 spec. in DEIC; Karagaitau, Narynsk, 1 spec. in MHNG; Przewalsk, Issyk-kul, 2 spec in HNHM; Ferganah, Osch, 7 spec. in ZHMB; Turk., Osch, Sammlung Stöcklein, 1 spec. in MHNG.; USSR, Kirgizia, Central Tjan-Shan, Naryngebiet, Flusstal Kara-Kuldschur, 3100 m, VII.–IX.1934, 3 spec. in DEIC; Ala Arča, 2100 m, Kirgiz. chrebet [mts], 6.–9.VII.1976, Josef Král lgt., 4 spec. in DKCP; USSR, Kirgizia, Ala Arča, Kirg. chrebet [mts], 11.7.1979, 2300 m, Mir. Dvořák lgt., 1 spec. in RCCP; USSR, Kirgizia bor., Issyk-Ata, 7.82, Ing. Z. Pokorná lgt., 1 spec. in RCCP; USSR-Kirghizia, 12.–15.7.85, Terskei Ala Too Mts., 30 km SSW Przewal'sk, Dzhety Oguz valley, 3700 m, Karel Majer leg., 2 spec. in DKCP, 101 spec. in NHMB; USSR, Kirgizia bor., Gor. Maevka, 7.87, Ing. S. Pokorný lgt., 5 spec. in RCCP; SU, Kirgizia, Kirgizskiy Ala Too [mts], Ala-Archa vall., 2100–2500 m, 1.–18.7.'88, coll. D. Král, 2 spec. in DKCP, 37 spec. in NHMB; SU, Kirgizia, Kirgizskiy Ala Too [mts], 42°23' [N] / 74°48' [E], Issyk-Ata-Yu vall., 3500 m, 1.8.'88, coll. D. Král, 2 spec. in DKCP, 56 spec. in NHMB; USSR, Kirgizia, Tian Shan Mts., 3500 m, Terskej Alatoo Ridge, 30 km SW of Przhewalsk, Jeti Oguz, 28.6.89, Čechovský Petr lgt., 24 spec. in RCCP; Kirg., Issyk-kul reg., Barskau, 10–17.7.91, I. Jeniš lgt., 2 spec. in DKCP, 2 spec. in RCCP; SU, Kirgizia, Grigoryevka, Kungey Ala Tau [mts], 3000 m, 6.–10.7., 42°50' 77°15', M. Kafka lgt., 5 spec. in DKCP. **Uzbekistan**: Margelan, Staudgr., 1 spec. in DEIC; Turkest., Margelan, 2 spec. in ZHMB. Alai, Turkest, 1 spec. in DEIC; Alatau, VI.04, Fischer, 1 spec. in HNHM; Alatau, J. Sahlb., 1 spec. in ZHMB; Ala Tau Geb., E. Fischer, 1 spec. in DEIC; Buchara, Haberhauer, 1 spec. in DEIC; Kirgisen – St.[eppen], Conradt., 1 spec. in ZHMB; Turkestan, coll. Kraatz, 2 spec. in DEIC; Turkestan, Reitter, 3 spec. in HNHM, 3 spec. in ZHMB.

Diagnostic characters. Medium sized species (body length 6.2–7.6 mm), oblong, moderately convex, entirely dark brown to black, rarely chesnut brown (described as var. *daraignezi*) coloured species. Dorsal surface moderately shiny, entirely glabrous. Head trapezoidal, slightly convex at middle, anterior clypeal margin distinctly roundly sinuate, anterior angle rounded, clypeal convexity subobsolete, sutural tubercles absent, gena rounded, exceeding distinctly eye, clypeal surface coarsely and densely punctate, puctures separated by approximately once their diameter, anteriorly scarcely rugopunctate. Pronotum moderately convex, widely subparallel; anterior angle rounded, only slightly projecting anteriorly; side broadly rounded in anterior third, then nearly straigtht, slightly diverging to rounded posterior angle; basis regularly rounded, distinctly bordered. Pronotal punctation double, consisting of coarse and sparse, rather irregularly distributed punctures, intermixed with finer regularly distributed ones, separated by at least once their diameter (mostly about twice their diameter) at disc; coarser and closer, separated by mostly less than once their diameter, laterally. Scutellum triangulate, approximately as wide as long, punctate basally. Elytra moderately convex, slightly dilated posteriorly, with microreticulation; humerus denticulate; striae distinctly impressed, strial punctures slightly crenating interval margins; intervals almost flat superficially but distinctly punctate. Macropterous. Metasternal plate scarcely concave, moderately shiny, with several coarse, irregularly distributed punctures.

Ventromedial protibial edge with row of denticles; terminal spur of protibia in male stout, long, acute apically, bent anteroventrally; in female simply pointed. Apical margin of meso- and metatibia fimbriate with strongly unequal setae. Basimesotarsomere shorter than superior terminal spur, inferior terminal spur of mesotibia in male shortened and obliquely cut off, in female simply acute. Basimetatarsomere approximately equal to superior terminal spur and longer than next two tarsomeres combined. Aedeagus (Figs 13, 14).

Epipharynx (Fig. 1). Epitorma and pternotormae distinctly sclerotized, area of proplegmatium sclerotized, with slightly indicated apotormae. Helus basally with several sensillae and laterally with microtrichiae and 4–6 thick setae. Corypha with 6–7 short and thick setae. Chaetoparia with one row of long, thick setae. Chaetopedium in addition to numerous microtrichiae with 15–17 long, thick setae. Acroparia and acanthoparia covered with thin, medium sized setae. Apophoba and ipophoba covered with numerous microtrichiae. Nesium with double row of rather irregularly spaced sensillae.

Distribution. First record from China (Xinjiang); Middle Asia (Alai, Pamir and Tian Shan mts) (for more details about distribution see Nikolaev 1987, Nikritin 1974, Protsenko 1968, 1976) .

***Aphodius* (*Pseudacrossus*) *kalabi* sp. n.**

(Figs 2, 15, 16)

Type material. Holotype (male), allotype (female) and paratypes Nos 1–18 (females), Nos 19–26 (males), labelled: "China, E Qinghai prov. CHALAXUNG, 4000 m 19.7.1992 [p]"; paratype No 27 (male), labelled: "China, E Qinghai prov. pass ca 50 km SW of HEKA 22.–25.6.1992, 4700 m [p]. Holotype, allotype and paratypes Nos 1, 2, 5–8, 10–20, 22–24, 26 and 27 in DKCP; paratype No 3 in MNHN; No 21 in MRCD; No 4 in PBCV; Nos 9 and 25 in RCCP.

Description. Body length 6.5–7.4 mm (HT – 6.8 mm, AT – 7.1 mm). Oblong, moderately convex; dorsal surface shining, without microreticulation; colour chesnut brown, pronotum and ventral surface darker brown; dorsal surface entirely bare.

Male. Head trapezoidal slightly convex at middle. Anterior clypeal margin slightly upturned only near anterior angles, broadly sinuate at middle; anterior angle rounded, sides almost straight. Gena regularly rounded, distinctly exceeding eye. Clypeal surface slightly depressed only near anterior emargination. Clypeal convexity almost absent, sutural tubercles absent. Frontal suture indicated only by short line at each side, genal suture distinct. Clypeal and occipital surface coarsely, almost regularly punctate, punctures separated approximately by their diameter; in some specimens this punctation confluent with wrinkles near anterior and lateral margins. Frons a little sparsely and less coarsely punctate than clypeus.

Epipharynx (Fig. 2). Epitorma and pternotormae distinctly sclerotized, area of proplegmatium sclerotized, with slightly indicated apotormae. Helus basally with several sensillae and laterally with row of several sensillae. Corypha with 7–9 short, thick setae. Chaetoparia with one row of medium sized, rather thin setae. Chaetopedium with 5–7 thick setae, microtrichiae only sparsely spaced. Acroparia and acanthoparia covered with thin, medium sized setae. Apophoba and ipophoba covered with numerous microtrichiae. Nesium with double row of rather irregularly spaced sensillae.

Pronotum moderately convex, wide subparallel, scarcely narrowed anteriorly; anterior angle rounded, only slightly projecting anteriorly; side broadly rounded in anterior third, then nearly

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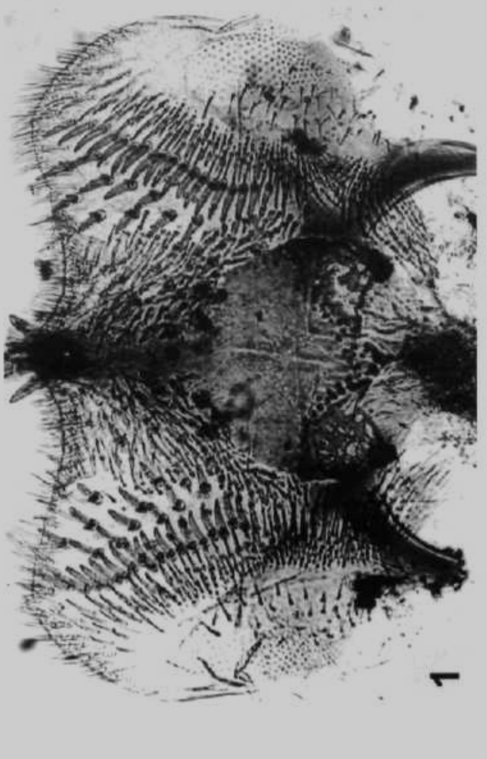
Figs 1–4. Epipharynx. *Aphodius* (*Pseudacrossus*) *grombczewskyi* D. Koshantschikov (Xinjiang, Bayanbulak) (1), *A.* (*P.*) *kalabi* sp. n. (PT No 27) (2), *A.* (*P.*) *nasutus* Reitter(Russia, Darasun) (3), *A.* (*P.*) *przewalskyi* Reitter (Qinghai, Ertala) (4). Scale – 0.3 mm.



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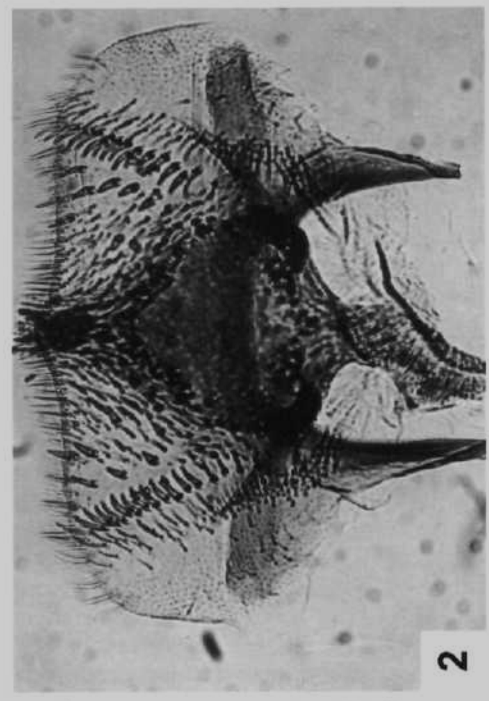

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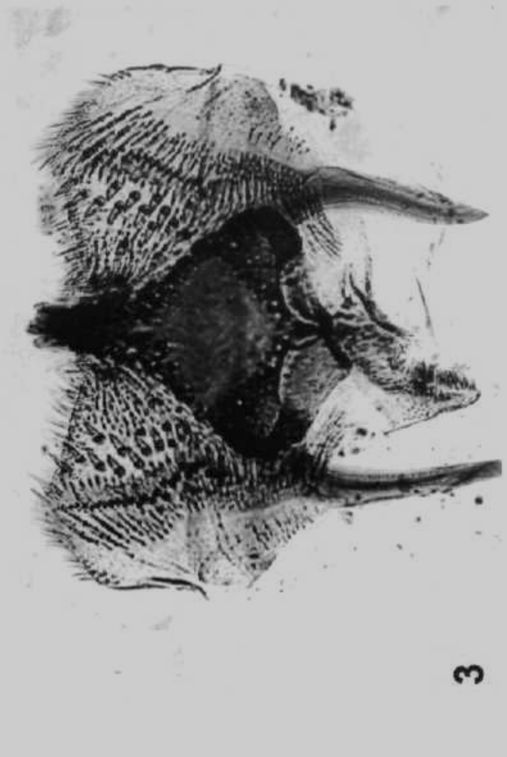

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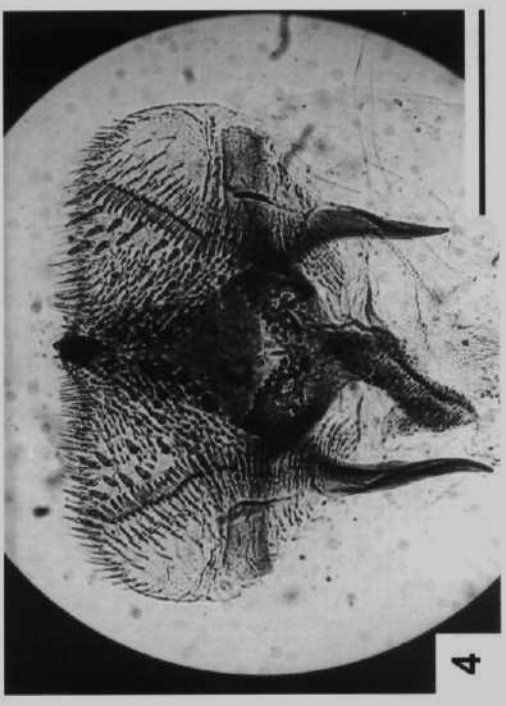

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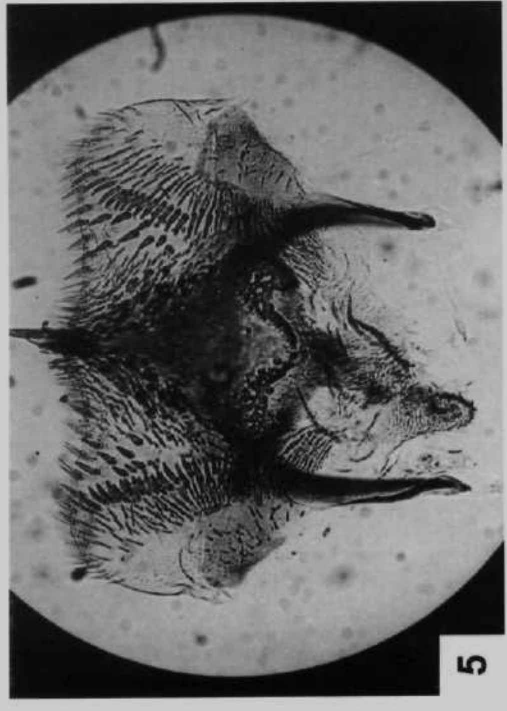

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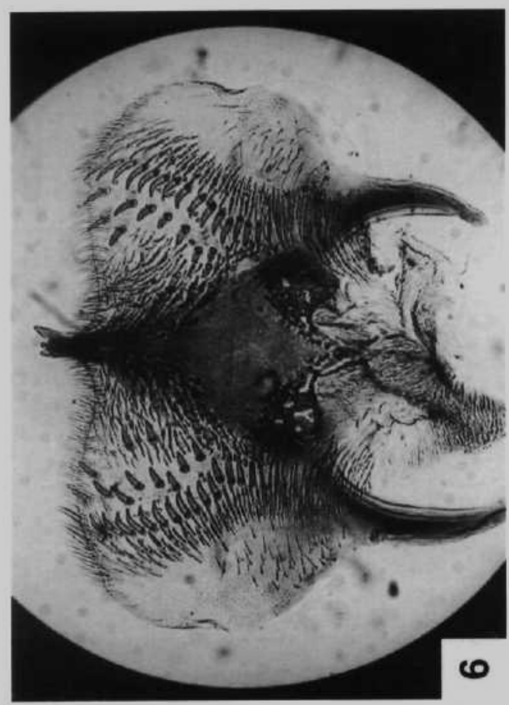

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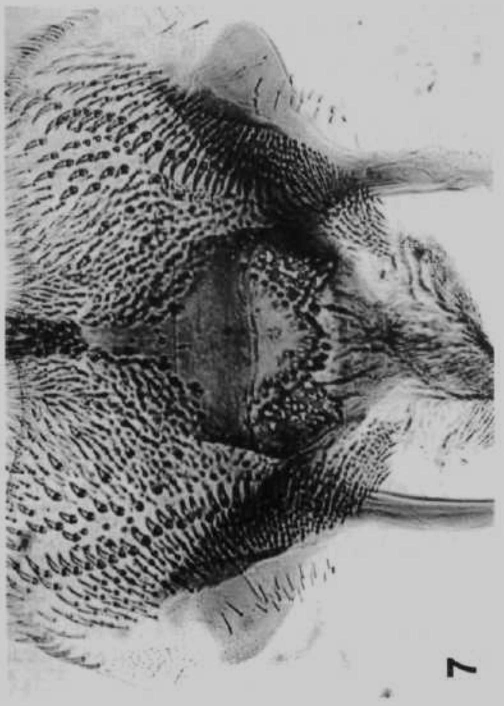
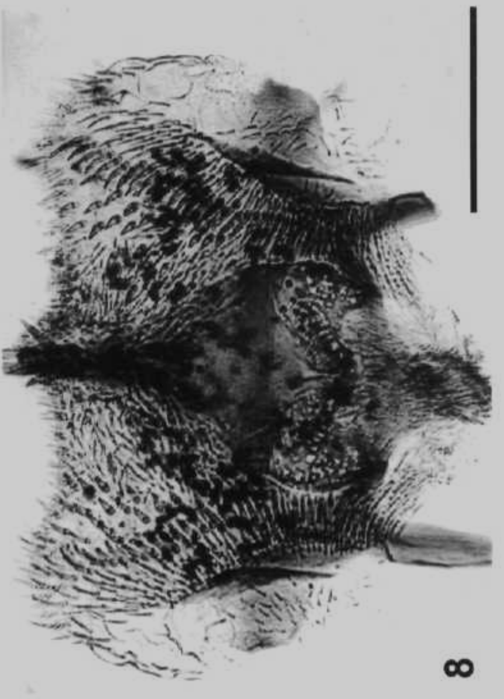


7



8

straight, slightly diverging to regularly rounded posterior angle; basis broadly rounded. Anterior margin without border. Anterior angle, lateral and posterior margin bordered, in some specimens border of posterior margin laterally indistinct. Punctation of pronotum double, consisting of coarse, sparsely and irregularly distributed punctures, intermixed with some fine ones; punctures separated by twice and more their diameter at disc, laterally punctation becoming only little closer (punctures separated at least by more than their diameter).

Scutellum triangulate, approximately as wide as long, with several coarse punctures basally.

Elytra moderately convex, slightly dilated posteriorly, widest behind middle, humerus finely denticulate. Striae narrow, distinctly impressed, strial puctures moderately deeply impressed, separated by more than their diameter, slightly crenating margins of intervals. Striae 1 and 10 completely developed, reaching nearly apex of elytra, stria 2 joining 9 just before apex, stria 3 a little shortened and joining stria 8, striae 4–7 shortened distinctly and confluent subapically. Stria 8 shortened distinctly before humerus. Intervals almost flat, wide, microscopically, irregularly, sparsely punctate. Sutural interval angustate apically.

Macropterous.

Metasternal plate scarcely concave, moderately shiny, with several coarse, irregularly distributed punctures bearing pale erected setae; longitudinal middline subobsolete. Abdominal sternites moderately shiny, shgreened, with pale setae.

All femora shiny, with coarse, irregularly distributed punctures. Protibia with three sharp external teeth and with row of external denticles in basal half; ventromedial edge with row of small denticles, 1–2 of them at middle more developed; terminal spur stout, long, acute apically, bent anteroventrally, inserting against emargination between apical and medial teeth, reaching approximately protarsomere 3. Apical margin and two well expressed transversal carinae of meso- and metatibia fimbriate with strongly unequal setae. Basimesotarsomere shorter than superior terminal spur, inferior terminal spur shortened and cut off. Basimetarsomere scarcely shorter than superior terminal spur and equal aproximately to next two tarsomeres combined.

Aedeagus as in Figs 15, 16.

Female differs from male by the following features: pronotal basis not bordered, metasternal plate entirely flat, terminal spur of protibia shorter, narrow and almost not bent anteroventrally, inferior terminal spur of mesotibia acute apically.

DIFFERENTIAL DIAGNOSIS. The new species is closely related to *A.* (*P.*) *grombczewskyi*, *A.* (*P.*) *przewalskyi* and *A.* (*P.*) *qinghaiensis* sp. n. (see the section Discussion). For the differentiation from related species see the complex of diagnostic characters in the key below.

COLLECTION CIRCUMSTANCES. All specimens were collected on open alpine pastures and grasslands at an altitude of about 4000–4700 m a. s. l. in dung of large herbivorous domestic mammals (*Bos*, *Equus*, *Ovis*).

NAME DERIVATION. Patronymic, named in honour of my colleague, Jaroslav Kaláb (Jinačovice u Brna, Czech Republic).

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Figs 5–8. Epipharynx. *Aphodius* (*Psudacrossus*) *qinghaiensis* sp. n. (PT No 9) (5), *A.* (*P.*) *subsericeus* Ballion (Kazakhstan, Orta-tau mts) (6), *A.* (*Qingaphodius* sbg. n.) *nikodymi* sp. n. (PT No 2) (7), *A.* (*Q.*) *ochotonarum* sp. n. (AT) (8). Scale – 0.3 mm.

***Aphodius (Pseudacrossus) nasutus* Reitter, 1887**

(Figs 3, 17, 18)

Aphodius (*Aphodius*) *nasutus* Reitter, 1887: 221.
Aphodius (*Pseudacrossus*) *nasutus*: Balthasar, 1964: 302, 307–308; Nikolaev & Puntsagdulam, 1984: 137–138, 157.
Aphodius (*Pseudagolius*) *nasutus*: Schmidt, 1913: 150; 1922: 233, 236; Boucomont, 1929: 782.
Aphodius (*Amidorus*) *consors* Reitter, 1892: 104 (syn. by Schmidt 1922).
Aphodius (*Amidorus*) *permodicus* Reitter, 1895: 208 (syn. by Schmidt 1922).
Aphodius (*Melinopterus*) *mehelyi* Csiki in Zichy, 1901: 108 (syn. by Schmidt 1922).
Aphodius (*Chilothorax*) *kelleri* W. Koshantschikov, 1911: 21–22; 1913: 265 (syn. by Schmidt 1922).
Aphodius (*Pseudagolius*) *necopinus* Balthasar 1932: 165 (syn. by Balthasar 1964).
Aphodius (*Melinopterus*) *Roschlapili* Csiki in Zichy, 1901: 108.
Aphodius (*Pseudagolius*) *nasutus* var. *roschlapili*: Schmidt, 1913: 150; 1922: 236.
Aphodius (*Pseudacrossus*) *nasutus* ab. *roschlapili*: Balthasar, 1964: 307; M. Dellacasa, 1988: 190, 395.

TYPE LOCALITY. Zaîdam [region], am Fusse des Burchan-Buda [mts] (Reitter 1887).

TYPE MATERIAL EXAMINED. *Aphodius* (*Pseudacrossus*) *nasutus*. Lectotype (male), by present designation: "Amdo 1884 Przevalsky [p] / Burch.[an] Buda [mts] 9–11000. [h] / Aphodius nasutus m. n. sp. [Reitter's MS]", in ZMAS.

Aphodius consors. Lectotype (male), by present designation: "Nordl. Mongolei Changai Leder [p] / coll. Reitter [p] / A. consors m. 1893 Nachtrag [Reitter's MS] / Holotypus 1892 Aphodius (Amidorus) consors Reitter [*]", in HNHM.

Aphodius mehelyi. Lectotype (male) and paralectotypes Nos 1–2 (males) and Nos 3–7 (females), by present designation: "Mongolia, Burgaltai [p] IX.5.1898 [h] / Exp. Zichy leg. Csiki [p] / A. Méhelyi Typus ! det Csiki [Csiki's MS] / Para-typus 1901 Aphodius (Melinopterus) Méhelyi Csiki [*]", all in HNHM.

Aphodius roschlapili. Lectotype and paralectotypes Nos 1–3 (females), by present desigantion: "Mongolia, Burgaltai [p] IX.5.1898 [h] / Exp. Zichy leg. Csiki [p] / A. Roschlapili Type ! Csiki [Csiki's MS] / Holotypus [resp.] Paratypus 1901 Aphodius (Melinopterus) Roschlapili Csiki [*]", all in HNNM.

Aphodius kelleri. Lectotype, female, by present designation: "Transbaicalien Urulga Keller [h] / Vol. Kelleri m. W. Koshantschikov [W. Koshantschikov's MS] / = consors Rttr. [Reitter's MS] / Paratypus 1911 Aphodius (Chilothorax) kelleri Koshantschikov [*]", in HNHM.

ADDITIONAL MATERIAL EXAMINED. **China, Qinghai**: Kuku-noor [= Qinghai lake]/ Reitter, 1 male in NMPC. **Mongolia**: Mongolia, Burgaltai, IX.5.1898 / Exp. Zichy, leg Csiki, 1 female in NMPC. Mongolia: Central aimak, Ulan Baator, Nucht im Bogdo ul, 1600m, 27.VIII.1965, Exp. Dr. Z. Kaszab, 2/2 in HNHM. **Russia**: Zabaykaliye Shilka, Mishrofanovo, 10.6.1896, F. Suvorov [label written in Cyrillic script], 1 male in ZMAS; ZSSR, Bajkal, ad. Irkutsk, 4.X.1960, leg. B. Pisarski, 2 spec. in MHNG; Russia, Transbaikalien, Tschita, 4.10.[19]71, 1 male in RCCP and 1 female in DKCP; USSR, X.1980, Irkutsk, Tunijev lgt., 1 male in DKCP; USSR, Transbaikal., Darasun, IX. 1984, leg. Shilenkov, 3/1 in HNHM.

DIAGNOSTIC CHARACTERS. Medium sized (body length 4.6–5.5 mm), oblong, convex, bicolorous species (elytra light to chesnut brown with dark spots, rarely spots confluent or missing, rest of body dark brown to blackish brown). Dorsal surface strongly shiny, entirely glabrous. Head semicircular, anterior clypeal margin deeply sinuate at middle, anterior angles rounded, clypeal sides regularly rounded up to rounded gena distinctly exceeding eye, clypeal convexity and frontal tubercles present, medial tubercle more expressed in male, in female tubercles subobsolete. Clypeal surface coarsely and densely punctate, punctures separated by less than their diameter. Pronotum convex; anterior angle rounded, only slightly projecting anteriorly; side broadly rounded in anterior third, then nearly straight and parallel (in male) or subparallel (in female); posterior angle rounded; basis regularly rounded, distinctly bordered. Pronotal punctation double, consisting of coarse and sparse, irregularly distributed punctures, intermixed with finer ones, separated by approximately twice their diameter. Scutellum triangulate, longer as wide, punctate basally. Elytra distinctly convex, slightly dilated posteriorly, without microreticulation; humerus without denticles; striae distinctly impressed, strial punctures remarkably crenating interval margins; intervals only very slightly convex, intervals punctation very sparse and fine. Macropterous. Metasternal plate flat, shiny, with medial longitudinal line, and laterally with several coarse punctures bearing setae. Ventromedial protibial edge with row of fine denticles; terminal spur of protibia in male stout, long, acute apically, bent anteroventrally, in female simple pointed. Apical margin of meso- and metatibia fimbriate with strongly unequal setae. Basimesotarsomere a little longer than superior terminal spur, inferior terminal spur of mesotibia in male shortened and obliquely cut off, in female simply acute. Basimetatarsomere a little longer than superior terminal spur and approximately equal to two next tarsomeres combined. Aedeagus (Figs 17, 18)

Epipharynx (Fig. 3). Epitorma and pternotormae distinctly sclerotized, area of proplegmatium only very slightly sclerotized. Helus basally with several sensillae, laterally with row of sensillae intermixed with 3–4 short, thick setae. Corypha with 5 short, thick setae. Chaetoparia with one row of medium sized, thick setae. Chaetopedium with numerous medium sized, thick setae, intermixed with numerous microtrichiae. Acroparia and acanthoparia covered with numerous thin, medium sized setae. Apophoba and ipophoba covered with numerous long and thin setae. Nesium with one row of fine short setae and laterally with group of numerous sensillae.

Distribution. China: "Tibet" (e. g. Balthasar 1964), Qinghai; Mongolia and Russia (Baikal region, Transbaikalia).

***Aphodius* (*Pseudacrossus*) *przewalskyi* Reitter, 1887**

(Figs 4, 19, 20)

Aphodius (*Acrossus*) *Przewalskyi* Reitter, 1887: 226.
Aphodius (*Pseudacrossus*) *przewalskyi*: Balthasar, 1964: 302, 309; Nikritin, 1974: 466; G. Dellacasa 1983: 392, 396–397, figs 915–918; M. Dellacasa 1988: 183, 395.
Aphodius (*Gonaphodius*) *Przewalskyi*: Reitter, 1892: 219, 240.
Aphodius (*Agolius*) *przewalskii* subsp. *przewalskii*: W. Koshantschikov, 1911: 205–209.
Aphodius (*Pseudagolius*) *przewalskyi*: Schmidt, 1913: 150; 1922: 233, 235; Boucomont, 1929: 782.

Type locality. Zuflüsse des Blauen Flusses [=Chang Jiang river], nämlich Kuntchum-tchu, Tchum-tcha-uma und By-djum (Reitter 1887).

Type material examined. Lectotype (male) and paralectotype (female), designated by G. Dellacasa (1983): "Amdo 1884 Przevalsky [p] / Syntypus [p, red label] / Lectotypus [resp.] Paralectotypus, Aphodius przewalskyi Rtt. des. G. Dellacasa 1981 [h]"; paralectotype (male), designated by G. Dellacasa (1983): "Aph. Przewalskyi m. 1887 Centr. Asien [Reiter's MS] / Syntypus [p, red label] / Paralectotypus Aphodius przewalskyi des. G. Dellacasa 1981 [h]"; all in ZMAS. 27 paralectotypes, by present designation: Nos 3–20 (males) and Nos 21–24 (females): "Amdo 1884 Przevalsky [p]", all in ZMAS; paralectotype No 25 (pinned male): "Amdo 1884 Przevalsky [p] / coll. Reitter [p] / Para-typus 1887 Aphodius (Acrossus) Przewalskyi Reitter [*] / Aphodius przewalskyi G. Dellacasa [det.] 1981 [h]", in HNHM; paralectotype No 26 (male): "Reitter [h] / Aph. Przewalskyi m. Central Asien [Reitter's MS]", in DEIC; paralectotypes Nos 27–29 (males): "Amdo 1884 Przevalsky [p] / coll. Kraatz [p]", in DEIC.

Additional material examined. **China, Sichuan**: China, Sichuan, Batang, 21.–22.7.1994, 14/9 in DKCP; China, NW Sichuan, Serxü, 4000 m, 20.6.1995, 2 males in DKCP and 5 males in JRCP; China, NW Sichuan, road Garzé-Barong, 25 km S Garzé, pass 3500 m, 10.7.1995, 1 male in DKCP and 2/2 in JRCP; Ch-NW Sichuan, ±3700 m, 32.59N 98.06E, 3.+15.7.1995, Serxü env., alpine meadow, 1 female in DKCP; Ch-NW Sichuan, 14/7.95, 33.09N 97.30 E, pass 15 km E Xiwu, 4000 m, alpine meadow, 1 female in DKCP. **Qinghai**: Amdo 1884 Przevalsky / Hoang-ho, $13^{1}/_{4}$ – 1400', 1male in ZMAS; Amdo 1884 Przewalsky / Burchan –Budda [mts], 1 spec. in ZMAS; China, E Qinghai prov., pass ca 50 km SW of Heka, 22.–25.6.1992, 4700 m, 1/1 in DKCP; China, E Qinghai prov., Huashixia, 4200 m, 27.6.1992, 2 males in DKCP; China, Quinghai, A'nyenmaqen Shan [mts], Huashixia, 28.–30.6.1994, 4200–4800 m, 37/20 in BZCL and 6/2 in DKCP ; China, E Qinghai prov., Qingshuihe, 4200 m, 1.–5.7.1992, 1/1 in DKCP; China, E Qinghai prov., Chalaxung, 4000 m, 19.7.1992, 10/23 in DKCP; China, E Qinghai prov., Ertala env., 3800 m, 22.–23.7.1992, 5/6 in DKCP; China, SE Qinghai, road Yushu-Toramarkog, pass 25 km SW Yushu, alpine meadows, 4500 m, 23.6.1995, 4/2 in DKCP and 12/6 in JRCP.

Diagnostic characters. Medium sized species (body length 6.0–7.5 mm), oblong, moderately convex; entirely chesnut brown to dark brown, rarely black coloured species, or in some specimens elytra light brown with dark spots. Dorsal surface moderately shiny, entirely glabrous.

Head trapezoidal, only very slightly convex at middle, anterior clypeal margin roundly sinuate, anterior angles rounded, clypeal convexity subobsolete, sutural tubercles almost absent, gena rounded, exceeding distinctly eye, clypeal surface coarsely and densely punctate, punctures separated by approximately once their diameter, scarcely rugopunctate anteriorly. Pronotum moderately convex, widely subparallel; anterior angle rounded, only slightly projecting anteriorly; side broadly rounded in anterior third, then nearly straight, slightly diverging to rounded posterior angle; basis regularly rounded, not bordered. Pronotal punctation double, consisting of coarse and very sparse, distinctly irregularly distributed punctures, intermixed with finer, irregularly distributed ones, separated by once to about twice their diameter at disc. Punctation becoming coarser and closer laterally, punctures separated by less than their diameter. Scutellum triangulate, approximately as wide as long, punctate basally. Elytra moderately convex, slightly dilated posteriorly, with microreticulation; humerus denticulate; stria distinctly impressed, strial punctures slightly crenating intervals margin; intervals flat, sparsely and superficially punctate. Macropterous. Metasternal plate scarcely concave, moderately shiny, with several coarse, irregularly distributed punctures. Ventromedial protibial edge with row of denticles; terminal spur of protibia in male stout, long, acute apically, bent anteroventrally; in female simply pointed. Apical margin of meso- and metatibia fimbriate with strongly unequal setae. Basimesotarsomere approximately equal to terminal spur, inferior terminal spur of mesotibia in male shortened and obliquely cut off, in female simply acute. Basimetatarsomere approximately equal to superior terminal spur and longer than two next tarsomeres combined. Aedeagus (Figs 19, 20).
EPIPHARYNX (Fig. 4).Epitorma and ptenotormae distinctly sclerotized, area of proplegmatium slightly sclerotized. Helus basally with two groups of longitudinally arranged sensillae, laterally with numerous microtrichiae. Corypha with 6–7 very short, thick setae. Chaetoparia with one row of medium sized setae. Chaetopedium in addition to numerous microtrichiae with 12–16 thick setae. Acroparia and acanthoparia with medium sized, thin setae. Apophoba and ipophoba covered with numerous microtrichiae. Nesium with one row of rather irregularly spaced sensillae.
DISTRIBUTION. China: "Tibet" (e. g. Balthasar 1964) Sichuan, Qinghai.

Aphodius (*Pseudacrossus*) *qinghaiensis* sp. n.
(Figs 5, 21, 22)

TYPE MATERIAL. Holotype (male), allotype (female) and 15 paratypes Nos 1–7 (males) and Nos 8–15 (females), labelled: "China, NE Qinghai prov., E Qilian Shan, 4200 m, OBO, 29.7.–1.8.1992 [p]"; 59 paratypes, labelled: Nos 16–27 (males) and Nos 28–53 (females): "China, NE Qinghai prov., OBO, E Qilian Shan 29.–30.7.1992, 4200 m [p]"; Nos 54–57 (males) and 58–64 (females): "China, E Qinghai prov., DAOTANGHE env., 3200 m, 25.–27.7.1992 [p]"; Nos 65–70 (males): "China, Qinghai reg., 3500 m, 120 km W of Qinghai Hu, Tianjum, 3.–4.7.1990 [p]"; Nos 71–73 (males) and No 74 (female): "China (Qinghai), Laji-shan Pass s. Xining, 3700–3900 m, 13.–15.VII.1993 [p]". Holotype, allotype, and paratypes Nos 1–4, 8–13, 16–19, 28–35, 54–60, 62–65 and 71–74 in DKCP; Nos 66 and 67 in MNCP; Nos 7, 15 in MNHN; Nos 5 and 61 in MRCD; Nos 27 and 53 in NMPC; Nos 6 and 14 in PBCV; Nos 20–26, 36–52, 68 and 69 in RCCP and No 70 in SJCP.

DESCRIPTION. Body length 6.2–7.7 mm (HT – 6.9 mm, AT – 7.4 mm). Oblong, moderately convex; dorsal surface weakly shining, without microreticulation; piceous, elytra in some specimens dark brown; elytra with microscopic setae.

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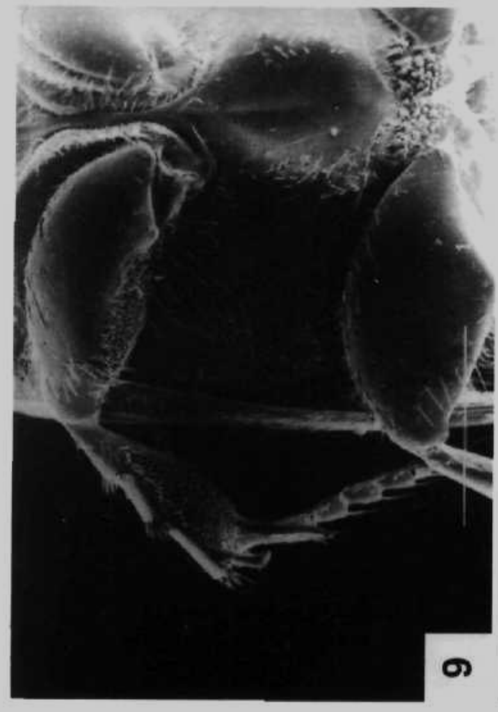
Figs 9–12. *Aphodius* (*Qingaphodius* sbg. n.) *nikodymi* sp. n., (PT No 2). Ventral aspect with metasternal plate, right midleg and right metafemur (9); *right midleg, ventral aspect (10), right metafemur, ventral aspect (11); rigth mesotibia, ventral* aspect (12).



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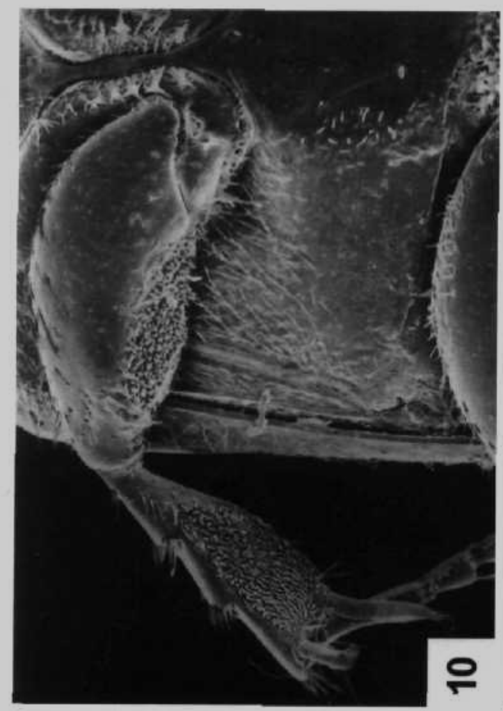

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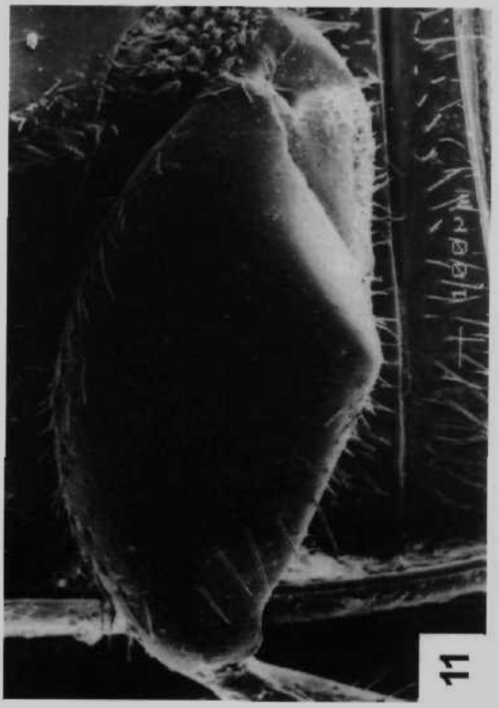

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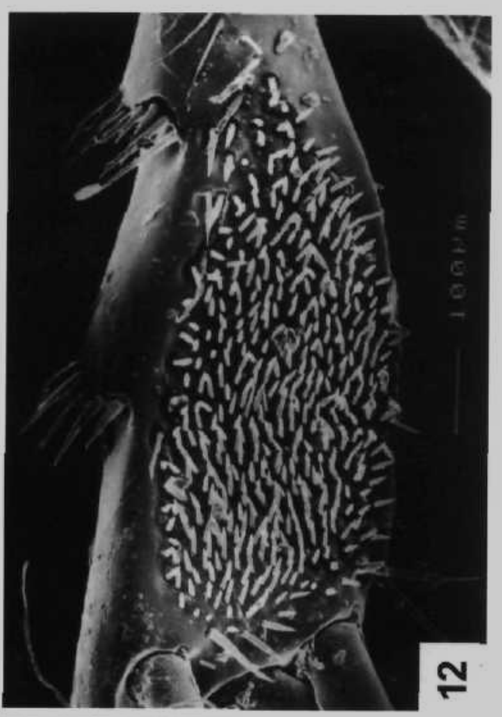

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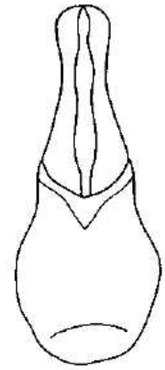
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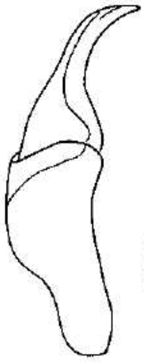
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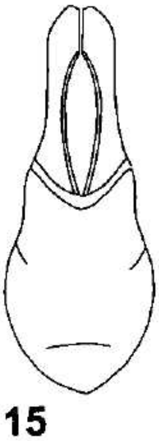
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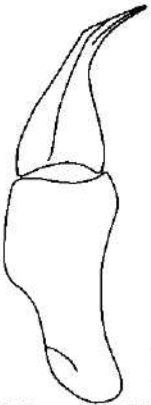
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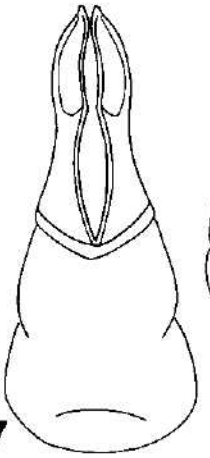
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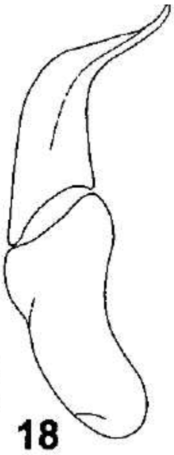
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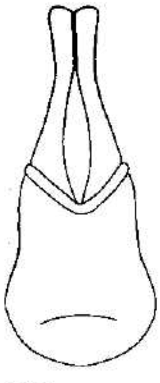
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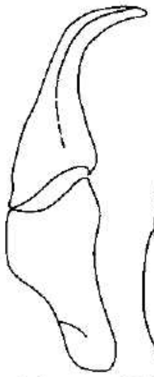
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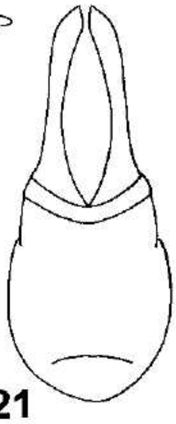
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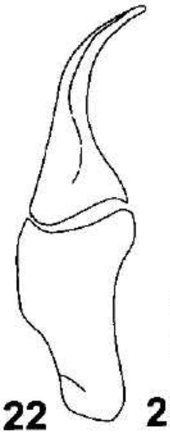
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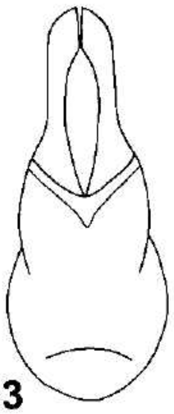
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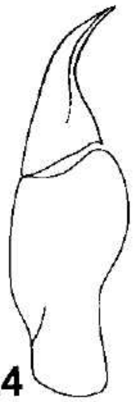
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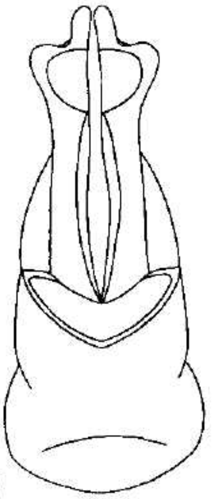
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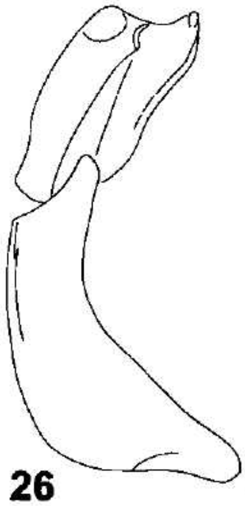
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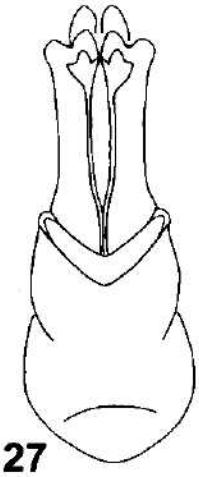
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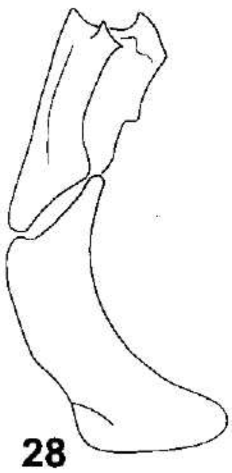
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Male. Head trapezoidal, slightly convex at middle, anterior margin of clypeus sinuate at middle, anterior angles rounded, sides almost straight, sinuate before gena, gena rounded, distinctly exceeding eye. Clypeal surface slightly depressed near anterior emargination, clypeal convexity almost absent; sutural tubercles obsolete. Clypeal surface near anterior margin and sides wrinkled, rest of head surface with simple, coarse punctures, separated approximately by their diameter.

Epipharynx (Fig. 5). Epitorma and pternotormae distinctly sclerotized, area of proplegmatium only very slightly sclerotized. Helus laterally with row of sensillae intermixed with 3–5 short setae. Corypha with 6–7 short, thick setae. Chaetoparia with one row of relatively long, thick setae. Chaetopedium with 12–14 short and thick setae, microtrichiae only sparsely spaced. Acroparia and acanthoparia covered with numerous thin, medium sized setae. Apophoba and ipophoba covered with numerous long, thin setae. Nesium with double row of rather irregularly spaced sensillae.

Pronotum moderately convex, wide subparallel, scarcely narrowed anteriorly; anterior angle rounded, slightly projecting anteriorly; side weakly diverging over anterior third, simply broadly rounded, posterior angle rounded; posterior margin projecting backwards with slight sinuation at each side. Anterior and posterior margin without border, lateral margin bordered. Punctation simple, coarse, dense, rather irregular, punctures separated by once to twice their diameter discally; at sides punctation becoming coarse and denser, with punctures separated by less than their diameter.

Scutellum triangulate, approximately as wide as long, distinctly punctate basally.

Elytra slightly widened behind middle, convex; humerus distinctly denticulate. Striae narrow, moderately deeply impressed; strial punctures slightly crenating margins of almost flat intervals. Stria 1 and 10 completely developed reaching nearly apex of elytron, stria 2 joining 9 just before apex, stria 3 a little shortened and joining stria 8, striae 4–7 shortened distinctly and confluent subapically. Stria 8 shortened distinctly before humerus. Surface of intervals with distinct, rather irregular, moderately impressed punctures. Sutural intrerval angustate apically.

Macropterous.

Metasternal plate scarcely concave, with coarse irregular punctures and with yellow setae laterally, midline indistinct. Abdominal sternites moderately shiny, shgreened, with pale setae.

All femora shiny, coarse, very sparse, irregularly punctate. Protibia regularly developed, with three sharp external teeth and with row of external denticles in basal half; ventromedial edge with row of small denticles, 1–2 of them at middle more developed; terminal spur stout, long, acute apically, bent anteroventrally, inserting against emargination between apical and medial teeth, reaching approximately anterior margin of protarsomere 2. Apical margin and two well expressed transversal carinae of meso- and metatibia fimbriate with strongly unequal setae. Basimesotarsomere approximately equal to superior terminal spur, inferior terminal spur shortened and cut off. Basimetatarsomere a little longer than superior terminal spur and approximately equal to next two tarsomeres combined.

Aedeagus as in Figs 21, 22.

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Figs 13–28. Aedeagus: odd numerals – dorsal aspect, even numerals – lateral aspect. *Aphodius* (*Pseudacrossus*) *grombczewskyi* D. Koshantschikov (Xinjiang, Bayanbulak) (13, 14), *A.* (*P.*) *kalabi* sp. n. (HT) (15, 16), *A.* (*P.*) *nasutus* Reitter (Russia, Darasun) (17, 18), *A.* (*P.*) *przewalskyi* Reitter (Qinghai, Ertala) (19, 20), *A.* (*P.*) *qinghaiensis* sp. n. (HT) (21, 22), *A.* (*P.*) *subsericeus* (Kazakhstan, Orta-tau mts.) (23, 24), *A.* (*Qingaphodius* sbg. n.) *nikodymi* sp. n. (HT) (25, 26), *A.* (*Q.*) *ochotonarum* sp. n. (HT) (27, 28).

Female differs from male by the following features: metasternal plate entirely flat, terminal spur of protibia shorter, narrow and almost not bent anteroventrally, inferior terminal spur of mesotibia acute apically.

Differential diagnosis. The new species is closely related to *A.* (*P.*) *grombczewskyi*, *A.* (*P.*) *kalabi* sp. n. and *A.* (*P.*) *przewalskyi* (see the section Discussion). For the differentiation from related species see the complex of diagnostic characters in the key below.

Collection circumstances. All specimens were collected on open alpine pastures and grasslands at an altitude of about 3000–4200 m a. s. l. in dung of large herbivorous domestic mammals (*Bos*, *Equus*, *Ovis*).

Name derivation. The specific name refers to the region of origin – the Qinghai province in China.

Aphodius (*Pseudacrossus*) *subsericeus* Ballion, 1878 comb. n.

(Figs 6, 23, 24)

Aphodius subsericeus Ballion, 1878: 283.

Aphodius (*Amidorus*) *subsericeus*: Schmidt, 1913: 148; 1922: 219, 226; Boucomont, 1929: 782; Endrödi, 1956: 75; Tesař, 1957: 250, 254–255; Balthasar, 1964: 288, 292–293; Nikritin 1973: 615; Nikolaev, 1987: 102, 119; M. Dellacasa, 1988: 204, 368.

Aphodius (*Amidorus*) *impolitus* Schmidt, 1909: 104 (syn. by Schmidt 1913).

Material examined. **China**, **Xinjiang**: *China, Xinjiang, ca 50 km NNE Narat, ca 10 km S Chokma, ca 2500 m 19/7.1993, 10* spec. in DKCP and 7 spec. in RCCP; Chan-Tengri, Mont. merid., 13 spec. in MHNG; Chine, Chines. Tian-Shan, v. Bodemayer, 1 male in DEIC, 1 male in HNHM; 1 male in ZHMB; Juldus, 1 spec. in ZMAS; Kuldscha [=Yining], Juldus, coll. Reitter, 2 males in HNHM. **Kazakhstan**: Turkestan, Tekkes, Sary Tör, Almásy 1906, coll. Endrödi, 20 spec. in HNHM; O. Kasachstan, Tyschkan-Schlucht, 1990–2600 m, 9.6.[19]90, V. G. Dolin [lgt.], 1 male in NHMB; S. O. Kasachstan, Orta-Tau Geb.-Kette, Orta-Karagajly Schl., 2000–2400m, 6.–10.06.[19]91, 4 spec. in DKCP and 6 spec in NHMB; Thian-S., coll. Dr. J. Fodor, 1 spec. in HNHM; Thian-S., Musart, 2 spec. in ZHMB; Thian-Shan, Naryn-kol, 1 spec. in MHNG; Thian S., Tekesthal, 1 spec., in MHNG, 4 spec. in ZHMB; Tschulskai, Semirjetschensk, coll. Winkler, 1 spec. in RCCP.

Type locality. Kuldscha [=Yining] (Ballion 1878).

Diagnostic characters. Medium sized species (body length 5.8–7.0 mm), oblong moderately convex, entirely dark brown to black coloured species. Dorsal surface only very slightly shiny, glabrous. Head slightly convex at middle, anterior clypeal margin distinctly roundly sinuate, anterior angles rounded, clypeal convexity weakly expressed, sutural tubercles subobsolete in male, missing in female, gena rounded, exceeding distinctly eyes, clypeal surface shgreened and coarsely, densely punctate, punctures separated by approximately once their diameter. Pronotum moderately convex, widely subparallel; anterior angle rounded, only slightly projecting anteriorly; side broadly rounded in anterior third, then nearly straight, slightly diverging to rounded posterior angle; basis regularly rounded, distinctly bordered. Pronotal punctation double, consisting of coarse, rather irregularly distributed punctures, intermixed with finer ones, separated by approximately once to twice their diameter at disc, coarser and closer laterally. Scutellum triangulate, a little longer than wide, shgreened. Elytra moderatly convex, slightly dilated posteriorly; humerus distinctly denticulate; striae distinctly impressed, shiny, strial punctures remarkably crenating interval margins; intervals flat, distinctly shgreened, only with very fine and scarcely visible punctures. Macropterous. Metasternal plate scarcely concave, subopaque, marginally with several coarse, irregularly distributed punctures. Ventromedial protibial edge with row of fine denticles; terminal spur of protibiae in male long, stout, bent anterorventrally and apically acute, in female simply popinted. Apical margin of meso- and metatibia fimbriate with only scarsely unequal setae in male and with almost equal setae in female. Basimesotarsomere approximately equal to superior terminal spur, inferior terminal spur of mesotibia in male shortened and obliquely cut off, in female simply acute. Basimetatarsomere distinctly longer than superior terminal spur and longer than next two tarsomeres combined. Aedeagus (Figs 23, 24).

EPIPHARYNX (Fig. 6). Epitorma and pternotormae slightly but distinctly sclerotized, area of proplegmatium only very slightly sclerotized. Helus laterally with group of microtrichiae and row of 6–8 short, thick setae. Corypha with 6 short, thick setae. Chaetoparia with one row of long, robust setae. Chaetopedium covered with group of 13–15 short, thick setae and numerous microtrichiae. Acroparia and acanthoparia covered with numerous thin, medium sized setae. Apophoba and ipophoba covered with numerous long, thin setae. Nesium with one row of fine, short setae and laterally with group of numerous sensillae.

DISTRIBUTION. China: Xinjiang. Kazakhstan, Kyrgyzstan.

Key to the *Pseudacrossus* species known from China

1 (2) Elytral humerus without denticles. China: "Tibet", Qinghai; Mongolia, Transbaikalia. .... *A.* (*P.*) *nasutus* Reitter
2 (1) Elytral humerus denticulate.
3 (4) Elytra opaque, strongly shgreened, intervals impunctate. Pronotal basis bordered. Basimetarsomere longer than superior terminal spur. China: Xinjiang; Kazakhstan, Kyrgyzstan. .... *A.* (*P.*) *subsericeus* Ballion
4 (3) Elytra not shgreened, shiny or opaque, intervals punctate (in *A.* (*P.*) *przewalskyi* very finely but pronotal basis not bordered). Pronotal basis bordered or not. Basimetatarsomere equal or subequal to superior terminal spur.
5 (6) Whole surface of pronotum with very sparse double punctation, punctures also laterally separated by at least more than once their diameter. Dorsal surface strongly shiny, elytra chesnut brown. China: Qinghai. .... *A.* (*P.*) *kalabi* sp. n.
6 (5) Pronotum at least laterally with close punctation (punctures separated by their diameter). Dorsal surface moderately shiny or opaque, elytra mostly darker or pale with dark spots.
7 (8) Pronotum with basal border. China: Xinjiang; mountains of Middle Asia .... *A.* (*P.*) *grombczewskyi* D. Koshantschikov
8 (7) Pronotum basally not bordered.
9 (10) Elytra opaque, intervals flat, finely, sparsely and superficially punctate. China: "Tibet", Qinghai, Sichuan. .... *A.* (*P.*) *przewalskyi* Reitter
10 (9) Elytra moderately shiny, intervals slightly convex, punctation consisting of coarse, more dense and moderately impressed punctures. China: Qinghai. .... *A.* (*P.*) *qinghaiensis* sp. n.

Qingaphodius sbg. n.
(Figs 7, 8, 9–12, 25–28)

TYPE SPECIES. *Aphodius nikodymi* sp. n.

DIAGNOSIS. Medium sized species. Body elongate, subparallel, moderately convex.

Male. Dorsal surface entirely glabrous. Anterior clypeal margin distinctly upturned only near anterior angles. Gena distinctly exceeding eye. Frons with distinct transversal ridge and with obsolete convexity posteriorly. Epipharyngeal pternotormae and area of proplegmatium sclerotized, apotormae strongly sclerotized; helus laterally with group of numerous microtrichiae and longitudinal row of short, thick setae medially; corypha with group of robust setae; chaetoparia with one row of medium sized, robust setae; chaetopedium covered with group of short, thick setae, and with numerous microtrichiae; medially of chaetoparia group of of several very short, fine setae; acroparia and acanthoparia with numerous thin, medium sized setae; apophoba and ipophoba covered with numerous long and thin setae; nesium with fine, short setae and group of sensillae. Anterior angle and lateral margin of pronotum distinctly bordered, basal border more or less interrupted medially. Scutellum small, triangulate, longer than wide. Elytral humerus not denticulate, with 10 striae and flat, wide intervals. Macropterous. Both meso- and metafemur distinctly wider than profemur. Mesofemur posteroventrally with sinuated area covered with brush of dense, short, thick setae (Figs 9, 10). Posterior metafemoral margin with obviously developed protrusion at ca. 0.3 from basis (Fig. 11). Protibia distinctly tridentate, without row of denticles near basis; ventromedial edge simple, only in basal third feebly crenulate or with several small denticles; terminal spur simply acute, not remarkably long or stout. Apical margin and two well developed external transversal carinae of meso- and metatibia fimbriate with strongly unequal setae. Mesotibia remarkably thickened, ventromedially with brush of dense, short and thick setae (Fig. 12); inferior apical spur bent strongly inwards (Fig. 10). Claw strongly developed. Aedeagus of extraordinary shape (*Figs 25–28*).

Female differs from male in the following features: metasternal plate flat; meso- and metafemur only indistinctly wider than profemur, simply built (mesofemur posteroventrally without sinuated area covered with special setation, metafemur without posterior protrusion); mesotibia not thickened, without brush of dense, short and thick setae; inferior apical mesotibial spur stout, sharply pointed, not bent inwards.

Affinities. The new subgenus belongs to a group of subgenera sharing the following synapomorphies: anterior clypeal angle rounded, gena distinctly exceeding eye; anterior margin of pronotum not bordered, posterior angle of pronotum rounded, pronotal basis either not or incompletely bordered; scutellum small, triangulate; apical margin of metatibia with unequal setation (cf. Balthasar 1964: 21–24). The modified inferior terminal spur and similar morphology of epipharyngeal structures (setation of chaetoparia, chatopedium, acroparia and acanthoparia) show that the new subgenus could be placed near the subgenus *Pseudacrossus* (at least near the type species and to it closely related species). Extraordinarily manifested sexual dimorphism in both the new species (shape and setation of mesofemur, metafemur and mesotibia) seems to be an *unique autapomorphy not only within the mentioned above subgenera group but within the* framework of the whole genus *Aphodius*. Therefore they are placed into the new subgenus, *Qingaphodius* sbg. n. (see also the Discussion section below).

Name derivation. Denotes the geographic distribution (Chinese province Qinghai) and relevance to the genus *Aphodius*. Masculinum.

***Aphodius* (*Qingaphodius* sbg. n.) *nikodymi* sp. n.**

(Figs 7, 9–12, 25, 26)

Type material. Holotype (male), allotype (female) and 15 paratypes (males), labelled: "China, Qinghai reg., 3500 m, 120 km W of Qinghai Hu, Tianjun, 3.–4.7.1990 [p]". Holotype, allotype and paratypes Nos 1–3, 5 in DKCP, No 4 in MRCD, Nos 6–9 in RCCP, Nos 10–11 in SJCP, Nos 12–15 in MNCP.

Description. Body length 6.4–7.5 mm (HT – 7.4 mm, AT – 6.5 mm). Elongate, subparallel, moderately convex, dark chesnut brown coloured species, protibia, tarsus and head appendages somewhat lighter. Dorsal surface entirely glabrous, shining.

Male. Head trapezoidal, slightly convex at middle. Anterior clypeal margin distinctly upturned only near anterior angles, broadly sinuate at middle, anterior angles broadly rounded, sides nearly straight, only very slightly notched before gena, gena obtusely rounded, exceeding distinctly eyes. Clypeal surface widely impressed nearly along the whole extent of anterior margin. Frons with distinct transversal ridge anteriorly and with obsolete convexity posteriorly, frontal suture indicated only by short line at each side near eye, genal suture distinct. Clypeus and frons very sparsely, minutely, regularly punctate; punctures separated by more than twice their diameter, on occiput punctation becoming denser.

Epipharynx (Fig. 7). Epitorma, pternotormae and area of proplegmatium slightly but distinctly sclerotized, apotormae strongly sclerotized. Helus laterally with group of numerous microtrichiae, intermixed with several short, thick setae, and longitudinal row of short thick setae medially. Corypha with 9–11 robust, sharply pointed setae. Chaetoparia with one row of medium sized, robust setae. Chaetopedium covered with group of 16–19 short, thick setae and with numerous microtrichiae. Medially of chaetoparia group of several very short, fine setae. Acroparia and acanthoparia covered with numerous thin, medium sized setae. Apophoba and ipophoba covered with numerous long and thin setae. Nesium with one row of fine, short setae, and laterally with group of several sensillae.

Pronotum subtrapezoidal, weakly convex, scarcely narrowed anteriorly; anterior angle slightly projecting anteriorly, broadly rounded, side nearly straight, slightly diverging to broadly rounded posterior angle, basis regularly rounded; anterior angle, lateral margin and basis axcept of middle part distinctly bordered (interruption narrower than scutellar basis). Punctation double, consisting of coarse, deeply impressed, irregularly and sparsely distributed punctures intermixed with minute, regularly and sparsely distributed ones (about the same size and distribution as clypeal and frontal ones); laterobasal area almost without coarse punctures.

Scutellum small triangulate, longer than wide, with several coarse punctures basally.

Elytra moderately convex, slightly dilated posteriorly, widest behind middle, humerus not denticulate. Striae distinctly impressed, strial punctures distinct, separated by more than once their diameter, slightly crenating margins of elytral intervals. Striae 1, 2, 3 and 10 completely developed reaching nearly apex of elytra, stria 3 joining 8 and 9 just before apex, striae 4–7 shortened before apex and stria 4 and 7, and 5 and 6 joining together. Stria 8 shortened before humerus. Intervals flat, rather wide, microscopically sparsely and irregularly punctate. Sutural interval narrowed apically.

Macropterous.

Metasternal plate shiny, glabrous and smooth except of margin, without midline furrow, distinctly concave; margin with coarse punctures bearing pale erected setae. Abdominal sternites moderately shiny, wrikled, laterally with pale seate.

All femora shiny, both meso- and metafemur wider than profemur. Anterior and posterior margins of profemur with long, pale setae. Mesofemur posteroventrally with sinuated area covered with brush of dense, short and thick setae (Figs 9, 10). Posterior metafemoral margin with obviously developed protrusion at ca. 0.3 from basis (Fig. 11). Protibiae distinctly tridentate, without row of denticles near basis; ventromedial edge almost not armed, only at basal third with several indistinct denticles; terminal spur simply acute, with insertion aggainst emargination between medial and basal teeth, reaching about middle of protarsomere 2. Apical margin and two well developed external transversal carinae of meso- and metatibia fimbriate with strongly unequal setae. Mesotibia remarkably thickened, ventromedially with brush of dense, short and thick setae; basimesotarsomere shorter than superior apical spur, inferior apical spur bent strongly inwards apically (Figs 9, 12). Basimetatarsomere shorter than superior apical spur and equal to next two tarsomeres combined. Claw remarkably expressed and strongly curved.

Aedeagus as in Figs 25, 26.

Female differs from male in the following characters: metasternal plate flat; meso- and metafemur only indistinctly wider than profemur, simply built (mesofemur posteronentrally without sinuation and and brush of characteristic setae, metafemur without posterior protrusion); mesotibia not thickened, without brush of characteristic setae; inferior apical mesotibial spur stout, sharply pointed, not bent inwards.

DIFFERENTIAL DIAGNOSIS. The new species is closely related to *A.* (*Q.*) *ochotonarum* sp. n. For the differentiation of species from each other see the complex of diagnostic characters in the key below and different shape of parameres and epipharyngeal structures.

COLLECTION CIRCUMSTANCES. All the type specimens were collected from the openings of marmot burrows. Usually they were buried in loose soil at the bottom. According to the available literature (Bibikov 1968, Hoffmann et al.1993) only a single marmot species, *Marmota himalayana* (Hodgson, 1841) (Mammalia: Rodentia), is known to occur in the Qinghai province.

NAME DERIVATION. Patronymic, dedicated to my friend Milan Nikodým (Praha), an excellent student on Melolonthinae and Sericinae.

***Aphodius* (*Qingaphodius* sbg. n.) *ochotonarum* sp. n.**

(Figs 8, 27, 28)

TYPE MATERIAL. Holotype (male), allotype (female) and 4 paratypes (females), labelled: "China – Qinghai, A'nyemaqen Shan, Huashixia, 28.–30.6.1994, 4200–4800 m [p]". Holotype, allotype and paratype No I in DKCP, paratypes Nos 2–4 in BZCL.

DESCRIPTION. Body length 5.3–6.4 mm (HT – 6.1mm, AT – 6.3 mm). Elongate, subparallel, moderately convex, blackish brown coloured species, clypeal margin, anterolateral angle of pronotum, legs, elytral suture and head appendages somewhat lighter. Dorsal surface entirely glabrous, moderately shining.

Male. Head trapezoidal, slightly convex at middle. Anterior clypeal margin indistinctly upturned only near anterior angles, broadly sinuate at middle, anterior angles broadly rounded, sides broadly rounded anteriorly, posteriorly (before gena) sinuate, distinctly separated from gena, gena regularly rounded, exceeding distinctly eye. Clypeal surface impressed nearly along the whole extent of anterior margin. Frons with only slightly developed medial convexity, frontal suture indicated only by short line at each side, genal suture distinct. Clypeal surface very sparsely, minutely, nearly regularly punctate, punctation becoming on occiput denser and coarser.

Epipharynx (Fig. 8). Epitorma, pternotormae and area of proplegmatium distinctly sclerotized, apotormae strongly sclerotized. Helus laterally with group of several microtrichiae and longitudinal row of 5–7 short, thick setae medially. Corypha with 7–8 robust setae. Chaetoparia with one row of medium sized, robust setae. Chaetopedium covered with group of 18–21 short, thick setae and with numerous microtrichiae. Medially of chaetoparia several very short, fine setae. Acroparia and acanthoparia covered with numerous long and thin setae. Nesium with irregular double row of fine, short setae and several groups of sensillae laterally.

Pronotum subtrapezoidal, broader than elytral basis, weakly convex, scarcely narrowed anteriorly; anterior angle slightly projecting anteriorly, broadly rounded, side nearly straight, slightly diverging to broadly rounded posterior angle, basis regularly rounded, indistinctly crenulate; anterior angle, lateral margin and posterior angle (reaching to elytral stria 5) distinctly bordered. Punctation double, consisting of coarse, deeply impressed, sparsely and very irregularly distributed punctures, intermixed with minute also irregularly distributed ones.

Scutellum small triangulate, longer than wide, with several coarse punctures basally.

Elytra moderately convex, slightly dilated posteriorly, widest behind middle, humerus not denticulate. Striae distinctly impressed, strial punctures distinct, separated by approximately once their diameter, indistinctly crenating margins of elytral intervals. Striae 1, 2 and 10 completely developed reaching nearly apex of elytra, stria 2 joining 9 just before apex, stria 3 a little shortened and joining stria 8, striae 4–7 shortened distinctly and stria 4 and 7, and 5 and 6 joining together. Stria 8 shortened before humerus. Intervals almost flat, wide, microscopically, irregularly sparsely punctate. Sutural interval narrowed and convex apically.

Macropterous.

Metasternal plate shiny, glabrous and smooth except for marginal area bearing with several coarse punctures, without midline furrow, distinctly concave. Abdominal sternites moderately shiny, wrinkled, with pale setae.

All femora shiny, both meso- and metafemur wider than profemur. Anterior and posterior margin of profemur with long, pale setae. Mesofemur posteroventrally with sinuated area covered with brush of dense, short and thick setae. Posterior metafemoral margin with obviously developed obtuse protrusion at ca. 0.3 from basis. Protibia distinctly tridentate, without row of denticles near basis; ventromedial edge simple, only at basal third feebly crenulate; terminal spur simply acute, reaching about middle of protarsomere 2. Apical margin and two well developed external transversal carinae of meso- and metatibia fimbriate with strongly unequal setae. Mesotibia remarkably thickened; ventromedially with brush of dense, short and thick setae; basimesotarsomere shorter than superior apical spur; inferior apical spur bent strongly inwards. Basimetatarsomere equal to superior apical spur and equal to next two tarsomeres combined. Claws remarkably developed and strongly curved.

Aedeagus as in Figs 27, 28.

Female differs from male in the following features: metasternal plate flat; meso- and metafemur only indistinctly wider than profemur, simply built (mesofemur posteroventrally without sinuated area covered with characteristic setation, metafemur without posterior protrusion); mesotibia not thickened, without brush of dense, short and thick seate; inferior apical mesotibial spur stout, sharply pointed, not bent inwards.

Differential diagnosis. The new species is closely related to *A.* (*Q.*) *nikodymi* sp. n. For the differentiation of species from each other see the complex of diagnostic characters in the key below and different shape of parameres and epipharyngeal structures.

Collection circumstances. All type specimens were collected buried in soil under droppings of pikas near their burrows. According to the literature available (Hoffmann 1993) at least five different *Ochotona* species (Mammalia: Lagomorpha) are known to occur in the Qinghai province, some of them being sympatric.

Name derivation. Patronymic, dedicated to small lagomorph mammal, *Ochotona*, with that the life of new species is tied, and simultaneously to my daughter Kristýna and my friend Slávek Březina's daughter Zuzana, two little girls bearing a picturesque Czech name for pika, "pišťucha", as their nicknames.

Key to the *Qingaphodius* sbg. n. species

1(2) Relatively lighter coloured and larger species (6.4–7.5 mm). Clypeal sides nearly straight, only very slightly notched before gena. Punctation of pronotum double, consisting of less coarse, shallowly impressed, irregularly and very sparsely distributed punctures, intermixed with minute, regularly and sparsely distributed ones; laterobasal area almost without coarse punctures. Insertion of apical protibial spur against emargination between medial and basal external teeth. Basimetatarsomere a little shorter than apical spur of metatibia. Parameres of different shape (Figs 25, 26). China: Qinghai. .... *A.* (*Q.*) ***nikodymi*** sp. n.

2(1) Relatively darker coloured and smaller species (5.3–6.4 mm). Clypeal sides broadly rounded anteriorly, before genae sinuate, remarkably separated from genae. Punctation of pronotum double, consisting of very coarse, deeply impressed, sparsely and very irregularly distributed punctures intermixed with minute also irregularly distributed ones; laterobasal area also coarsely punctate. Insertion of apical protibial spur against medial external tooth. Basimetatarsomere equal to superior apical spur of metatibia. Parameres of different shape (Figs 27, 28) China: Qinghai. .... *A.* (*Q.*) ***ochotonarum*** sp. n.

DISCUSSION

Except for *Aphodius* (*Pseudacrossus*) *nasutus* the remaining five *Pseudacrossus* species so far known from China constitute a homogeneous group of closely related species (for more detail about morphology see the descriptions above). They all occur in relatively high mountainous areas and tend therefore to make locally different populations or subspecies. Three closely related and very similar allopatric taxa, *A.* (*P.*) *grombczewskyi* (Tian Shan), *A.* (*P.*) *przewalskyi* (Tibetan plateau in NW Sichuan and Qinghai) and *A.* (*P.*) *qinghaiensis* sp. n. (Qilian Shan Mts s. l.) can also be considered as subspecies. However, also closely related *A.* (*P.*) *kalabi* sp. n. is known to be sympatric and probably also syntopic with *A.* (*P.*) *przewalskyi* and *A.* (*P.*) *subsericeus* is sympatric with *A.* (*P.*) *grombczewskyi*. This facts favour rather the species status for all the five so far known species. In addition, our current knowledge of alpha-taxonomy, distribution and zoogeography of *Aphodius* species inhabiting these mountainous areas is too inadequate to satisfactorily resolve this problem. *A.* (*P.*) *nasutus* belongs to other species group (different shape of clypeal convexity, presence of distinct sutural tubercles on head, different epipharyngeal structures etc.) occurring Central and Middle Asia.

Both the new species, *A.* (*Qingaphodius* sbg. n.) *nikodymi* sp. n. and *A.* (*Q.* sbg. n.) *ochotonarum* possess the same interesting, extraordinary sexual dimorphism. Both the species are tied with small mammals (*Marmota* or *Ochotona*, respectively). Thus, they are probably exclusively dependent by their feeding on relatively small excrements. Their mating activity probably occurs in free space (not inside of or under large excrements), either at the burrow entrance, or in shallow pits, which are the animals resting in. This is, as a matter of fact the only site with its microclimate (enhanced temperature and humidity, absence of wind) move favourable than that of the surrounding landscape. The place of the occurrence is an Alpine, rather flat biotope, free of forest, exposed to strong wind, particularly in spring months, and to drastic continental temperature changes. The striking sexual dimorphism has been thus probably developed to help the pair to keep the computation position under the rough climatic conditions. This theory is also supported by the presence of the long, anchor-shaped paramere making possible the firm coupling of the mating pair.

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BOOK REVIEW

HAUSMANN K. & HÜLSMANN N. (eds.): **Progress in Protozoology. Proceedings of the IX International Congress of Protozoology. Berlin 25–31 July 1993**. Stuttgart-Jena-New York: Gustav Fischer Verlag, 1994.136 pp. Format 210×287 mm. Hardcover, price *DM 128.–*. *ISBN 3–437–30762–2. US ISBN 1–56081–397–0*

This volume reflects the actual state of knowledge of free-living and parasitic protozoa when presenting lectures and summaries of the IX International Congress of Protozoology. The Congress was organized by the German Society of Protozoology (duly supported by the German Societies for Parasitology and Tropical Medicine) on behalf of the International Commission of Protozoology. Both editors are at the Institute of Zoology, Free University of Berlin. The list of contributors contains 34 international experts. More than 800 participants from 50 countries came to Berlin, thus continuing a series which was initiated 32 years ago in Prague. In the contents six plenary lectures, 20 symposia's reports and two video sessions are listed.

Particular lectures present scientific reports illustrated by figures, schemes and photomicrographs, and concluded with a list of selected references to the primary literature. Unfortunately, some manuscripts have not been submitted. The volume provides insights into the morphology, ultrastructure, cell biology, physiology, biochemistry, molecular biology, evolution, life cycles, and ecology of protozoa. Also applied aspects of vaccination and diagnosis, chemotherapy and chemoprevention of protozoan infections are looked at.

The series of **plenary** lectures starts with a report on protozoan evolution and systematics when discussing ultrastructural and molecular studies. The logic of phylogenetic reconstruction, construction of skeletal tree, the concepts of *protists* and *protistology*, and classification schemes are presented here. In following lectures the cytoskeleton and molecular basis of pattering in ciliates, and progress in some anti-protozoan vaccines are looked at. There is an actual overview of opportunistic protozoa in AIDS, such as genera *Pneumocystis, Leishmania, Toxoplasma, Cryptosporidium* and *Isospora*, also the *Microsporidia – Enterocytozoon bieneusi, Encephalitozoon cuniculi, E. hellem, Septata intestinalis* and *Pleistophora* sp. This series concludes with information on new technologies in protozoan research.

The **Symposia** present scientific reports or groupings of brief communications. Topics covered include vaccination against human and animal protozoic pathogens, functional aspects of organelles in parasitic protozoa, recognition and cell-interaction, protistan ecology and pollution, life cycles of parasitic protozoa, chemotherapy and chemoprevention, motility, behaviour, and orientation. Following reports deal with cultivation of parasitic protozoa, with the cytoskeleton of protists, with molecular perspective on evolution, control of the cell cycle, protists of anaerobic environment, with intracellular traffic, host-symbiont interactions, mechanisms of pathogenicity among parasitic protozoa, and finally with protozoan links in food webs. In video productions on protozoa demonstrated are the optoelectronic and laser microbeam imaging, phototaxis and chemokinesis in ciliates, *Balamuthia mandrillaris* causing amoebic encephalitis, finally the movement of cilia and flagella, and plasmodial protists of the sea.

Multi-authored by leading experts, this attractively produced monograph is intended for those who want to update their knowledge in the field of general, medical and veterinary protozoology.

Jindřich Jíra

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Quaternary birds of the Baikal region, East Siberia

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Abstract. Avian remains were described from one mid-Pleistocene and 10 late Pleistocene to Holocene localities of the Baikal region in Siberia. Together, 21 species were identified. Most of them still inhabit the area, but *Apus melba* has now its nearest known locality in western Kirghizia, and *Struthio asiaticus* became extinct.

Aves, late Quaternary, East Siberia

INTRODUCTION

The Quaternary history of the bird fauna of the Baikal region in Siberia is rather poorly known yet. Previously, bird remains were mentioned from the middle Pleistocene locality Zasuchino in Zabajkal'e (Kalmykov 1986), and late Pleistocene archaeological sites of Mal'ta and Krasnyj Jar' in the Angara basin (Ermolova 1978), and Bol'šoj Jakor' in the Vitim basin (Belousov et al. 1990). Ermolova (1978) reported also on a few bird remains from the Holocene archaeological sites of Lenkovka (Mesolithic), and Rutino and Serovo (Neolithic). All of them lay in the Angara basin. East of Lake Baikal, only undated (Pleistocene to Holocene) eggshell remains of the extinct ostrich *Struthio asiaticus* Milne-Edwards, 1871 were described, mostly from surface dune deposits (Tugarinov 1930a,b, 1933, Sosnovskij 1932, Ivan'ev 1958a,b, 1964, Ivanov 1960, Gajdučenko & Tivanenko 1978, Imetchenov & Kalmykov 1988, Michajlov & Kuročkin 1988).

In the present paper, we report on the avian remains from one mid-Pleistocene, and 10 late Pleistocene to Holocene localities of the Baikal region. These bird remains are deposited in the Buryat Institute of Social Sciences, Ulan-Udè (loc. Ust'-Kjachta 17), and in the Buryat Geological Institute in Ulan-Udè (all other localities). Avian taxa are arranged according to Voous (1977). Minimum numbers of individuals were calculated after Grayson (1984). Bird remains were identified by J. Mlíkovský, stratigraphical data are by F. Chenzychenova and A. Filippov. For accompanying mammal faunas see Chenzychenova et al. (1991), and Chenzychenova (1994, in prep.).

RESULTS

1. Igetej

LOCALITY. At Bratsk dam, Irkutsk Province, Russia. The bones were collected in 1990 by F. Chenzychenova from the upper part of grey sands underlaying cultural horizons. Age of the locality is younger half of the the Middle Pleistocene, according to the morphology of *Dicrostonyx* and *Lagurus* teeth (Chenzychenova 1994).

BIRD FAUNA. Cf. *Calidris* sp.: distal part of a juvenile tarsometatarsus, belonging to a very small species; MNI = 1. The identification is tentative. *Passeriformes* indet.: several bones of very small, mostly juvenile passerines. Two partial premaxillae belong to a single species of an unidentified insectivorous bird. MNI = 2.

2. Mal'ta (Transeja)

LOCALITY. At Belaja river, Irkutsk Province, Russia. The bones were collected in 1993 by F. Chenzychenova and G. Šuspanova from grey dayish soil. Estimated age is the end of the late Pleistocene.

BIRD FAUNA. *Lagopus lagopus* (Linnaeus): mandible, furculum, femur dex., 4 tibiotarsi sin., 4 tarsometatarsi (3 sin., 1 dex.); MNI = 3.

3. Char'jaska 2

LOCALITY. In Tugnuj basin, Republic of Buryatia, Russia. The bones were collected in 1986 and 1987 by F. Chenzychenova from grey sandy loam. Two layers were distinguished, both dated at the end of the late Pleistocene.

BIRD FAUNA (upper layer). *Fringilla montifringilla* Linnaeus: prox. part of humerus dex.; MNI = 1.

BIRD FAUNA (lower layer). *Passeriformes* indet.: A few bones of small passerines.

4. Ust'-Kjachta 17

LOCALITY. In Kjachta County, Republic of Buryatia, Russia. The bones were collected in 1992 by F. Chenzychenova and V. Tašak in black sandy loam from layer 3 (cultural horizon). Age of the layer has been radiometrically estimated at 11 600 ± 155 years BP (SO AN 3091, Tašak 1993).

BIRD FAUNA. *Struthio asiaticus* Milne-Edwards, 1871: eggshell fragments (Tašak 1993). *Delichon urbica* (Linnaeus): humerus dex.; MNI = 1.

5. Kurtun 1

LOCALITY. On Ol'chon island, Irkutsk Province, Russia. The bones were collected in 1991 by F. Chenzychenova and I. Grebnev from layer 1 of these cave deposits. They are Holocene in age.

BIRD FAUNA. *Lagopus lagopus* (Linnaeus): tarsometatarsus dex.; MNI = 1.

6. Brekčievaja

LOCALITY. At Kitoj river, Irkutsk Province, Russia. The bones were collected in 1986 and 1989 by A. Filippov, A. Kutuzov and O. Morozov from red clays (cave deposits) at the depths of 0–10 cm (layer A), and 50–90 cm (layer B). They are Holocene in age.

BIRD FAUNA (layer A). *Tetrao tetrix* Linnaeus: scapula dex.; MNI = 1. *Columba* sp.: coracoid sin., humerus sin.; MNI = 1. The bones fall in the size class of *Columba livia* Gmelin and *Columba rupestris* Pallas, both of which occur in the area. These species cannot be distinguished osteologically and, moreover, are recently known to interbreed widely (Berezovikov & Ščerbakov 1990, Doržiev 1991, Fomin & Bold 1991). *Apus melba* (Linnaeus): 2 humeri (1 sin., 1 dex.); MNI = 1. Greatest length of the measurable humerus was 17.4 mm.

BIRD FAUNA (layer B). *Falco* cf. *tinnunculus* Linnaeus: prox. part of humerus sin.; MNI = 1. *Tetrao tetrix* Linnaeus: dist. part of coracoid sin., dist. part of ulna sin.; MNI = 1. *Gallinago* sp.: prox. part of humerus sin.; MNI = 1. The bone appears to be slightly larger than that of *Gallinago gallinago* (Linnaeus).

7. Tonta

Locality. At Tonta river, Irkutsk Province, Russia. The bones were collected in 1987–1989 by A. Filippov from cave deposits of gruss, rock debris and brown soil at depth of 1.5–1.8 m. They are late Holocene in age.

Bird fauna. *Hirundo rustica*: humerus dex., dist. humerus dex, prox. ulna, 4 juv. tarsometatarsi; MNI = 2.

8. Kadilinskaja

Locality. In Primorskij Range, Irkutsk Province, Russia. The bones were collected in 1989 by A. Filippov from cave deposits of gruss, rock debris and dark brown and grey soils. Several layers were discerned, including bird-yielding Nr. 4 (Ka-68), 5 (Ka-21), 7 (Ka-72), and 6–8 (Ka-87), all of which are late Holocene in age.

Bird fauna. *Hirundo rustica*: Ka-21: coracoid dex., prox. coracoid sin., prox. humerus sin., dist. humerus dex., carpometacarpus sin., prox. carpometacarpus sin.; MNI = 2. Ka-68: 2 carpometacarpi sin. (1 juv.), 8 juv. tarsometatarsi; MNI = 5. Ka-72: tarsometatarsus; MNI = 1. Ka-87: juv. tarsometatarsus; MNI = 1.

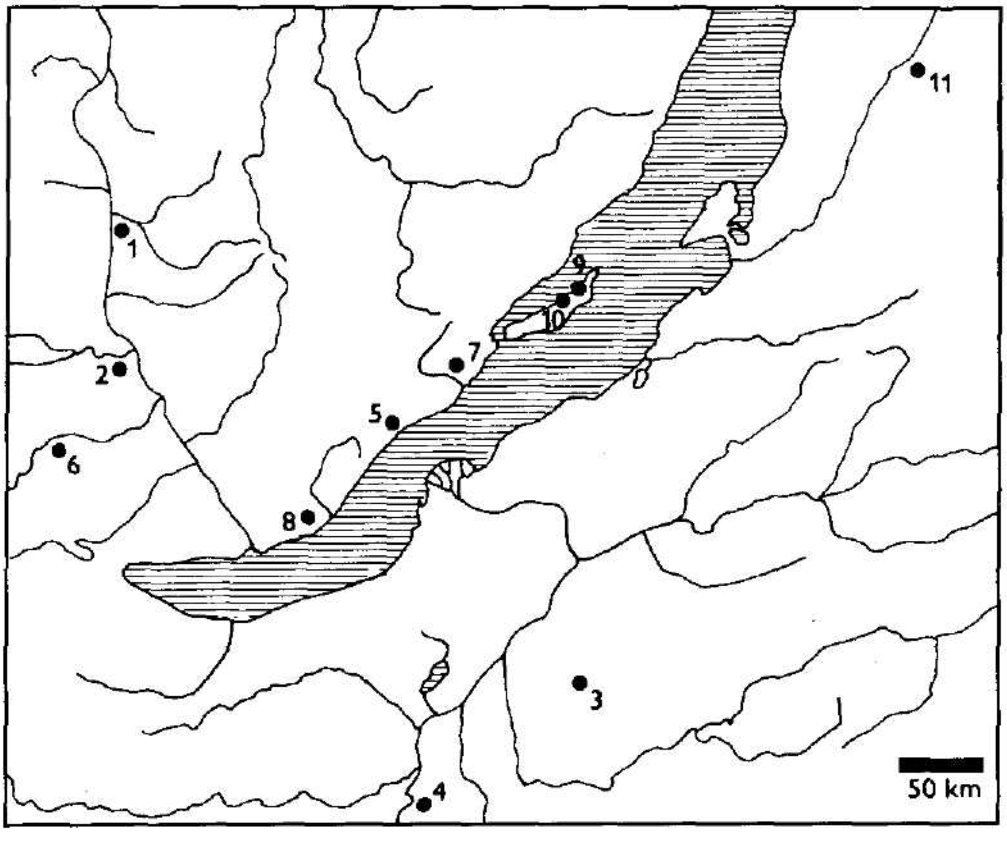

Fig. 1. Quaternary avian localities in the Baikal region, East Siberia. 1 – Igetej, 2 – Mal'ta, 3 – Char'jaska 2, 4 – Ust'-Kjachta 17, 5 – Kurtun 1, 6 – Brekčievaja, 7 – Tonta, 8 – Kadilinskaja, 9 – Šamanskaja, 10 – Boro-Chuchan, 11 – Barguzin Valley.

9. Šamanskaja

LOCALITY. On the Ol'chon island in Lake Baikal, Irkutsk Province, Russia. The bones were collected in 1989 by A. Filippov from cave deposits of light brown clays and sands with gruss. Bird yielding layers include those at the depths of 0–0.1 m (surface, Ša-33), 0.7–0.8 m (Ša-22), and 0.8–0.9 m (Ša-16). They are late Holocene in age.

BIRD FAUNA (Ša-33). *Corvus monedula*: carpometacarpus sin.; MNI = 1.

BIRD FAUNA (Ša-22). *Actitis hypoleucos*: coracoid dex.; MNI = 1.

BIRD FAUNA (Ša-16). *Carpodacus erythrinus*: humerus dex.; MNI =1. *Carduelis* sp.: symphysial part of mandible, belonging to a small species; MNI = 1.

10. Boro-Chuchan

LOCALITY. On Ol'chon island, Irkutsk Province, Russia. The bones were collected in 1989 by A. Filippov from cave deposits with gruss, rock debris and brown-grey soils. Their age was estimated at 2500–4000 years BP.

BIRD FAUNA. *Falco tinnunculus*: dist. humerus dex.; MNI = 1. *Corvus monedula*: carpometacarpus sin.; MNI = 1.

11. Barguzin valley

LOCALITY. At Barguzin river, Republic of Buryatia, Russia. The bones were collected in 1981 and 1984 by M. Erbaeva and F. Chenzychenova from undated (late Pleistocene – Holocene) surface dune deposits at two sites, called Kilometer 122, and Kilometer 125.

BIRD FAUNA (Kilometer 122). *Anas* sp. (large): prox. parts of 2 coracoidea sin., 2 carpometacarpi dex.; MNI = 2. *Anas* sp. (small): carpometacarpus sin.; MNI = 1. *Aythya* cf. *ferina* (Linnaeus): coracoid sin., prox. part of coracoid sin.; MNI = 1. *Fulica atra* Linnaeus: dist. part of tarsometatarsus dex.; MNI = 1.

BIRD FAUNA (Kilometer 125). *Circus cyaneus* (Linnaeus): dist. part of tarsometatarsus sin.; MNI = 1. Anatidae indet.: phalanx I digiti majoris; MNI = 1. *Pica pica* (Linnaeus): prox. part of humerus sin.; MNI = 1.

DISCUSSION

Avian remains recovered from the late Pleistocene to Holocene localities at Lake Baikal are too scarce so far to allow for taphonomical or ecological interpretations. Also, none of the investigated bones has shown any pathological modifications.

One record is highly interesting from the zoogeographical point of view. Two humeri of *Apus melba*, found in the Holocene deposits of Brekčievaja cave, mean that the area of this swift was much more expanded in the near past. Today, this species is distributed in the Palearctic from SW Europe to Kirghizia, where it is a typical bird of south Palearctic mountains (Stepanjan 1990). This record indicates, that the ornithogeographic classifications of south Palearctic mountains, which are based on Recent distributional data (Beme 1975, Banin 1988), may be biased by Holocene extinctions.

One of the species, *Struthio asiaticus*, is extinct. This ostrich was widespread in Asia till the Holocene (Lambrecht 1933, Burčak-Abramovič 1953). Its distribution has never been mapped properly, but the data available indicate, that *S. asiaticus* reached in the Quaternary the northern border of its distribution at 53° N near Bogatovsk in Kujbyšev Province in the European part of Russia (Pidopličko & Goldin 1964), and at 52° N at southern Lake Baikal in Siberia (various localities; Tugarinov 1930a,b, 1933, Sosnovskij 1932, Ivan'ev 1958a,b, 1964, Ivanov 1960, Gajdučenko & Tivanenko 1978, Imetchenov & Kalmykov 1988, Michajlov & Kuročkin 1988, Tašak 1993, this paper). It is unknown, when the ostrich disappeared from the Baikal region. Tašak (1993) documented, that it lived there at least till the latest Pleistocene (ca. 11 600 yr BP). Gajdučenko & Tivanenko (1978) provided evidence, that the ostrich survived in the Lake Baikal region till the Holocene, but their record is not dated more closely. On the other hand, there is no historical record of the ostrich in this region (Bold et al. 1991, Fomin & Bold 1991).

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A review of the genus *Odochilus* (Coleoptera: Aphodiidae: Odochilinae)

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Abstract. Five new species of the genus *Odochilus* Harold, 1877 are described as follows: *O. parasyntheticus* sp. n., *O. parasetosus* sp. n., *O. parajohnsoni* (all from the Philippines), *O. thailandicus* sp. n. (from Thailand) and *O. sarawakensis* sp. n. (from Sarawak). The formerly described subspecies *O. syntheticus philippinensis* Rakovič, 1987 is considered as a good species. The genus *Odochilus* is divided into two subgenera – the nominotypical subgenus and *Odochilus* (*Parodochilus*) sbg. n. Keys to species are presented. Illustrations of new species are provided. Relationships between particular species and their distribution are discussed.

Taxonomy, new subgenus, new species, new combinations, keys, Coleoptera, Scarabaeoidea, Aphodiidae, *Odochilus*, Oriental region

The present review of the genus *Odochilus* Harold, 1877 is prevalently based on studying very interesting material received for study and identification from four Czech entomologists (Dr Svatopluk Bílý, Dr David Král, Dipl Ing Radek Červenka and Mgr Aleš Bezděk), and on reexamining material in the author s collection and in the Dr Balthasar's collection (National Museum, Praha). The author is greatly indebted to these colleagues and to Dr Josef Jelínek, who made him possible to study material in the National Museum, Praha.

The following acronyms stand for collections, which are the specimens quoted below kept in:

ABCB	– Czech Republic, České Budějovice, Aleš Bezděk collection
DKCP	– Czech Republic, Praha, David Král collection
MRCD	– Czech Republic, Dobřichovice, Miloslav Rakovič collection
RCCP	– Czech Republic, Praha, Radek Červenka collection

Subgenera of the genus *Odochilus*

The genus *Odochilus* currently includes 15 species (with taking into account the five new species described below). Out of them, 8 species have medially interrupted, however, otherwise quite continuous fourth pronotal ridge (see Figs 1–7). On the other hand, in the other 7 species, this pronotal ridge is broken into longitudinal formations each side of the medial interruption (see Figs 8–13). This difference is very striking. The two groups are easy to separate from each other without any transition within this, otherwise unusually homogeneous, genus. Thus, the consideration of the two groups as subgenera is proposed here as follows:

Key to subgenera

1 (2) Fourth pronotal ridge medially interrupted and thus divided into left and right branches, however, otherwise simple, continuous. Upper edge of each branch forming a monotonic, continuous line extended laterally from the medial interruption (Figs 1–7). .... *O.* (*Odochilus*)

2 (1) Fourth pronotal ridge also interrupted medially, however, both (left and right) parts never monotonic – arranged in short, rather longitudinal formations (small keels or elevated areas), either discrete or each fused with neighboring ones, thus forming a „zig-zag" line each side of the medial interruption (Figs 8–13). .... *O.* (*Parodochilus*) sbg. n.

Odochilus (*Odochilus*) Harold, 1877

TYPE SPECIES. *Odochilus syntheticus* Harold, 1877: 62–63.

Based on the examination of material, as mentioned in the introduction, the following three species are described here, and one species (formerly described as a subspecies) is recognized as a good species.

Odochilus (*Odochilus*) *parasyntheticus* sp. n.

(Fig. 2)

Small (2.5 to 3.0 mm), oblong oval, moderately broader behind, matte, brown.

Head granulate anteriorly, posteriorly with two pairs of oblique ridges and distinct longitudinal, arched ridge above each eye (Fig. 2). Granulae mostly small, rounded, medially arranged in two parallel rows. Clypeus rounded (not emarginate) anteriorly. Eyes large, well visible from above. Genae notched, protruding (Fig. 2). Very small, dust-like setae situated throughout marginal zone of genae and along ridges above eyes.

Pronotum transversal (length-to-width ratio of 1:1.545), with four sharp transverse ridges, bisinuate laterally (Fig. 2). First to third ridges continuous, fourth ridge interrupted medially. Small longitudinal ridges adjacent to lateral ends of third and fourth transverse ridges. Small, dust-like setae mostly situated along small longitudinal keels, posterior transverse ridges and pronotum lateral margins. Posterior corners and posterior margin of pronotum with apically moderately dilated setae. Upper edge of transverse ridges with fine pore-like punctures. Areas between transverse ridges with fine transverse wrinkles.

Scutellum small, triangular. Elytra slightly broader behind, length-to-width ratio 1:0.685, with ten striae and ten intervals. Striae wide, with large, deep, rectangular punctures. Odd intervals high, sharp, strongly costate, even intervals lower, slightly costate (tenth interval only posteriorly slightly costate, anteriorly flat). Epipleura and odd elytral intervals with short, dust-like setae.

Tibiae slim, tarsites slim, subcylindrical, claws small, hornlike.

Ventral surface also matte, dark brown. Metasternum only slightly impressed medially, with narrow, anteriorly shortened furrow, metasternal plate glabrous. Abdominal sternites glabrous, pygidium with four setae. Anterior femur wide, with row of medium-sized setae behind anterior margin and row of rather thin setae along posterior margin. Intermediate and posterior femora slim, with four rows of semidecumbent setae along anterior margin and on ventral surface and two larger, erect setae on posterior margin, each trochanter with one long seta.

TYPE MATERIAL. *Holotype: Philippines, 200 m, SW Panay, 8 km E of Bontol, 10.–11. Dec. 1990, Bolm lgt. – in RCCP;* paratype 1: Philippines, Panay, 10 km E Sibalom, 10. Dec. 1990, 100 m, Bolm lgt. – in DKCP; paratype 2: the same data as with paratype 1 – in MRCD.

NAME DERIVATION. Based on a similarity of many character with the allopatric species *O. syntheticus*.

Differential diagnosis. The *O. parasyntheticus* sp. n. can be differentiated from the other species of the genus based on the key to species presented below. The closely allied sympatric species *O. philippinensis* has a much deeper posterior emargination of the pronotum lateral margin. Even elytral intervals are rather weaker (lower and narrower) in the present species.

***Odochilus* (*Odochilus*) *parasetosus* sp. n.**

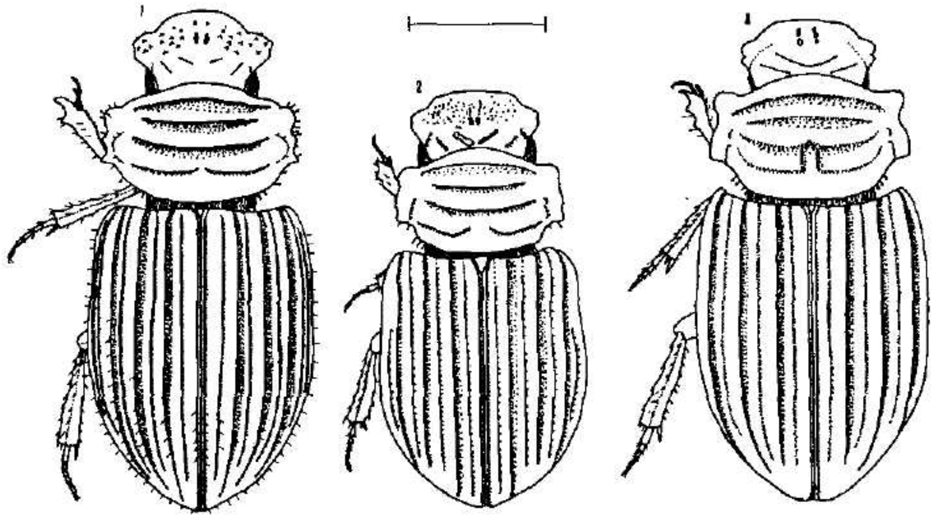
(Fig. 1)

Small (2.9 mm), oblong oval, moderately broader behind, matte, dark brown (Fig. 1).

Head anteriorly with small granulae bearing short setae, posteriorly with two pairs of oblique ridges, in front of oblique ridges with pair of longitudinal keels. Clypeus rounded (not emarginate) anteriorly. Genae large, moderately notched, eyes well visible from above.

Pronotum transversal (length-to-width ratio 1:1.556), with four distinct, sharp transverse ridges, first to third ridges continuous, fourth ridge interrupted medially; with short longitudinal setae-bearing keels at ends of third and fourth ridges. Lateral margin with two distinct emarginations, with moderately, however, distinctly apically dilated setae. Posterior margin with slightly dilated setae.

Scutellum small, triangular. Elytra moderately elongate, length-to-width ratio 1:0.711, with ten wide striae and ten narrow intervals. Odd intervals high, costate, equipped with long, erect, apically moderately dilated setae. Even intervals lower, however, still costate throughout (except for flat tenth interval), glabrous.



Figs 1–3. Body shape and structure of three new species of *Odochilus* (*Odochilus*) Harold. 1 – *O.* (*O.*) *parasetosus* sp. n.; 2 – *O.* (*O.*) *parasyntheticus* sp. n.; 3 – *O.* (*O.*) *parajohnsoni* sp. n. Scale line 1 mm.

Tibiae and tarsi slim, anterior tibia with three distinct teeth. Tarsites slightly to moderately widened apically. Upper terminal spur of metatarsus slightly shorter than first metatarsite. Lower terminal spur hardly as long as 1/2 of first metatarsite. Claws small, hornlike.

Ventral surface also dark brown, matte. Metasternum moderately impressed medially, with narrow, anteriorly shortened longitudinal furrow, with about six medium-sized setae on metasternal plate each side of the furrow. Each abdominal sternite with transverse row of six to eight setae. Pygidium with four setae. Anterior femur wide, with two rows of setae (along anterior and posterior margins). Intermediate and posterior femora slim, with four longitudinal rows of setae, each intermediate and posterior trochanter with one long, acute seta.

Type material. Holotype: Philipp., Mindanao, Siocom, X–1974, V. Bruno – in MRCD.

Name derivation. Based on the closest relationship to the species *O. setosus*.

Differential diagnosis. Only two species -- the *O. setosus* and *O. parasetosus* sp. n. have their odd elytral intervals with long, erect setae. The two species differ from each other in three characters, as shown in the key to species.

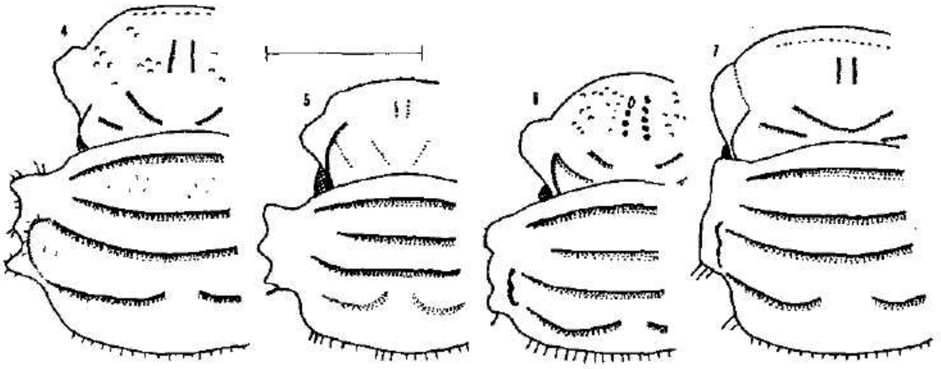
Odochilus (*Odochilus*) *parajohnsoni* sp. n.

(Fig. 3)

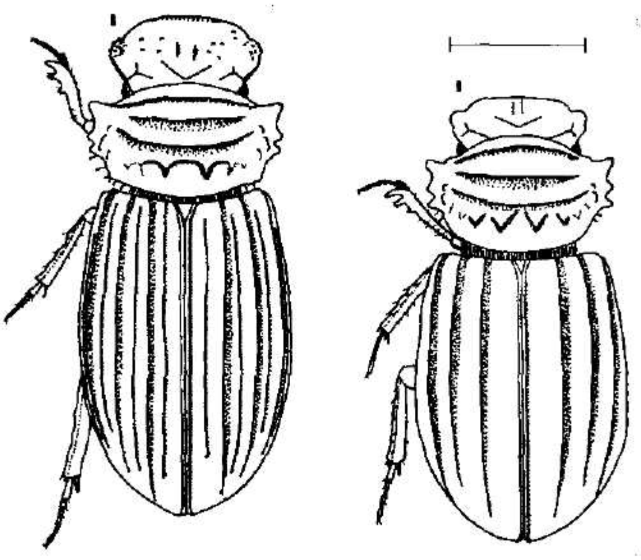
Small (2.7 to 3.0 mm), oblong oval, moderately broader behind, matte, dark brown (Fig. 3).

Head anteriorly with rather uneven, however, not distinctly granulate surface, posteriorly with V-shaped swelling and pair of oblique ridges. Pair of longitudinal keels consisting of discrete granules in front of V-shaped swelling (Fig. 3). Genae distinctly notched, moderately protruding beyond eyes. Eyes visible from above.

Pronotum transversal (length-to-width ratio 1:1.43), with four transverse, strongly convex, however, not quite sharp ridges; first to third ridges continuous, fourth ridge interrupted medially, with longitudinal elevations extended from this interruption forward to third ridge; small longitudinal keels present at ends of posterior ridges (Fig. 3). Lateral margins with small, hardly perceptible, dust-like setae, strongly emarginate anteriorly, posterior emargination nearly missing.



Figs 4–7. Shape and structure of head and pronotum of four formerly described species of *Odochilus* (*Odochilus*) Harold. 4 – *O.* (*O.*) *setosus* Boucomont; 5 – *O.* (*O.*) *haroldi* Rakovič; 6 – *O.* (*O.*) *syntheticus* Harold; 7 – *O.* (*O.*) *johnsoni* Rakovič. Scale line: 0.5 mm.



Figs 8–9. Body shape and structure of two new species of *Odochilus* (*Parodochilus* sbg. n.). 8 – *O.* (*P.*) *sarawakensis* sp. n.; 9 – *O.* (*P.*) *thailandicus* sp. n. Scale line: 1 mm.

Scutellum small, triangular. Elytra moderately elongate, length-to-width ratio 1:0.711, with ten striae and ten intervals. Intervals moderately costate (except for flat tenth interval), odd intervals considerably higher than even ones, with short, dust-like setae, even intervals glabrous, surfaces of intervals quite matte, with considerable microreticulate structure. On elytron disk, odd intervals as wide as striae and wider than even intervals.

Tibiae slim, anterior tibia with three distinct teeth, tarsites only slightly widened apically. Upper terminal spur of metatibia slightly shorter than first metatarsite. Lower terminal spur hardly as long as 1/2 of first metatarsite. Claws small, hornlike.

Ventral surface also matte, dark brown. Metasternum moderately impressed medially, with narrow, anteriorly shortened furrow. Abdominal sternites bare except for one seta on each lateral margin of sixth sternite. Pygidium with two setae. Anterior femur wide, with row of thin setae along posterior margin and rather indistinct setae on ventral surface. Intermediate and posterior femora with one long seta on posterior margins, with indistinct rows of small setae on ventral surface, each trochanter with one long, apically slightly dilated seta.

TYPE MATERIAL. Holotype: Philippines, Panay, 10 km E Sibalom, 10. Dec. 1990, Bolm lgt., 100 m – in DKCP; paratype 1: the same data – in DKCP; paratype 2: the same data – in MRCD.

NAME DERIVATION. Based on the closest relationship to the species *O. johnsoni*.

DIFFERENTIAL DIAGNOSIS. By its not quite sharp pronotal ridges, the present species is allied only to the sympatric species *O. johnsoni*. The two species can be differentiated from each other based on three characters, as shown in the key to species.

Odochilus (*Odochilus*) *philippinensis* Rakovič, 1987 species propria

Odochilus syntheticus philippinensis Rakovič, 1987: 34.
Odochilus syntheticus philippinensis: Stebnicka 1993: 32.

The present author has formerly described this taxon (Rakovič 1987) as a subspecies of *O. syntheticus* with respect to only relatively weak differences observed. The present study of many further specimens of the genus made him possible to recognize the fact that characters described here are very constant or, in other words, there is only a very slight individual variability within each species of the genus. In addition to this, a further closely related species is described here – *O.* (*O.*) *parasyntheticus* sp. n., which is sympatric with the *O.* (*O.*) *philippinensis* and thus, the differences in characters of the three related species should be considered at the specific and not infraspecific level.

Material examined. 3 paratypes: Plains of NE Leyete Is., P.I., Nov 44–Jan 45, Darlington, paratype, Odochilus syntheticus philippinensis sp. n., M. Rakovič det 1986 – in MRCD.

Odochilus (*Odochilus*) *setosus* Boucomont, 1914

Odochilus setosus Boucomont, 1914: 344.

In the revision of the genus (Rakovič 1987), three specimens of *O. setosus* were examined (all from Kalimantan) – 1 specimen labeled „S.O. Borneo". During the present work, further 9 specimens were studied (also from Kalimantan).

Material examined. 4 specimens: Indonesia, Kalimantan W., Nanga Saraval env., Tontang, 24.7.–2.8., J. Schneider lgt. 1993 – in DKCP; 2 specimens: the same data – in MRCD; 3 specimens: the same data – in RCCP.

Odochilus (*Odochilus*) *bacchusi* Rakovič, 1987

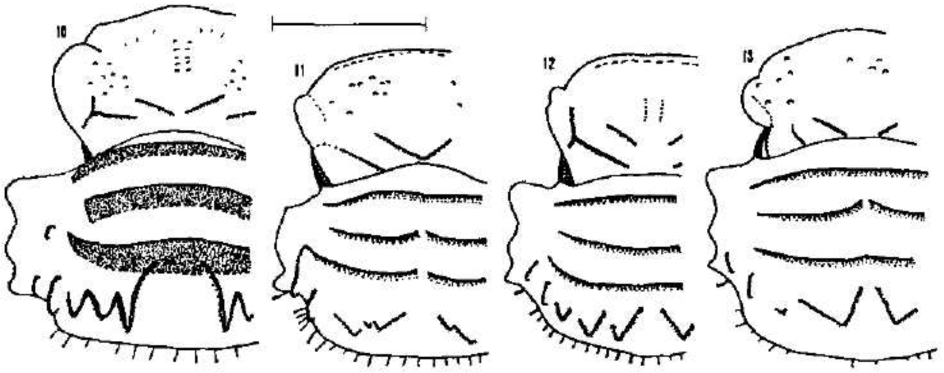
Odochilus bacchusi Rakovič, 1987: 40.

Total of 15 specimens of this species were formerly studied by the present author (Rakovič 1987) – all from N. Borneo. One further specimen from Sabah was studied in the present work.

Material examined. 1 specimen: Malaysia, Sabah range, Ranau env., 1.–2.8. 1985, K. Maruyama lgt. – in DKCP.

Key to species of the subgenus *Odochilus*

1 (4) Odd elytral intervals with long, erect setae.
2 (3) Even elytral intervals subcostate throughout. Pronotum lateral margins with clavate setae. Setae on head very short, nearly dust-like. 2.9 mm. The Philippines. .... *O.* (*O.*) *parasetosus* sp. n.
3 (2) Even elytral intervals flat in anterior 1/3. Setae on pronotum lateral margins at most negligibly dilated apically. Setae on head shorter than those on pronotum, however, rather long – distinctly erect. 3.1 to 3.4 mm. Kalimantan. .... *O.* (*O.*) *setosus* Boucomont
4 (1) Odd elytral intervals with short, dust-like setae.
5 (6) Elytra narrow at their base, much broader behind. Fourth pronotal ridge weak (Fig. 5). 2.8 mm. Kalimantan. .... *O.* (*O.*) *haroldi* Rakovič
6 (5) Elytra subparallel. Fourth pronotal ridge essentially as high as first to third ones.
7 (10) Anterior pair of oblique ridges on head replaced by V-shaped swelling (Figs 3 and 7). Pronotal ridges strongly convex, however, not quite sharp.
8 (9) Third pronotal ridge consisting of two medially convergent branches (Fig. 3). Vestigial, however, distinct pair of longitudinal ridges present medially between third and fourth ridges (Fig. 3). Elytral intervals with microreticulate structure making their surface distinctively different from that between punctures in elytral striae. 2.7 to 3.0 mm. The Philippines. .... *O.* (*O.*) *parajohnsoni* sp. n.



Figs 10–13. shape and structure of head and pronotum of four formerly described species of *Odochilus* (*Parodochilus* sbg. n.). 10 – *O.* (*P.*) *buruensis* Boucomont; 11 – *O.* (*P.*) *bacchusi* Rakovič; 12 – *O.* (*P.*) *balthasari* Rakovič; 13 – *O.* (*P.*) *pittinoi* Rakovič. Scale line: 1 mm.

9 (8) Third pronotal ridge rather in form of monotonic arch (Fig. 7). No medial longitudinal ridges present on pronotum (Fig. 7). Microreticulate structure of elytral intervals indistinct, their surface essentially similar to that observed between punctures in elytral striae. 3.0 to 3.6 mm. The Philippines. .... *O.* (*O.*) *johnsoni* Rakovič
10 (7) Head vertex with two pairs of oblique ridges. Pronotal ridges sharp.
11 (12) Pronotum lateral margin weakly bisinuate – mainly posterior emargination shallow (Fig. 3). 2.5 to 3.0 mm. The Philippines. .... *O.* (*O.*) *parasyntheticus* (sp. n.)
12 (11) Pronotum lateral margin strongly bisinuate, posterior emargination deep (Fig. 6).
13 (14) Longitudinal ridges on clypeus short, but very distinct and continuous. Lateral longitudinal keels at ends of third and fourth pronotal ridges divided into two discrete parts. 3.0 to 3.4 mm. The Philippines. .... *O.* (*O.*) *philippinensis* Rakovič
14 (13) Longitudinal ridges on clypeus weak, consisting of discrete granules. Short longitudinal keels at ends of third and fourth pronotal ridges only notched. 3.0 to 3.4 mm. Sulawesi. .... *O.* (*O.*) *syntheticus* Harold

Parodochilus sbg. n.

TYPE SPECIES. *Odochilus balthasari* Rakovič, 1987: 37.

Descriptions of two new species are presented below, found in the material studied.

Odochilus (*Parodochilus*) *sarawakensis* sp. n.
(Figs 8, 14)

Small (3.1 to 3.3 mm), oblong oval, moderately broader behind, matte, dark brown (Fig. 8). Head more or less distinctly granulate anteriorly (granulae on clypeus less distinct, those on genae more distinct), posteriorly with V-shaped swelling and pair of oblique ridges, posterior ridges extended forward up to swellings above eyes. Pair of vestigial longitudinal ridges in front of V-swelling. Clypeus rounded (not emarginate), anteriorly. Genae large, rounded, eyes well visible from above.

Pronotum transversal, length-to-width ratio 1:1.460, with four transverse ridges, first-to-third ridges sharp, continuous, fourth ridge broken into longitudinal formations (Fig. 8). Furrows between ridges with either longitudinal or transverse wrinkles. Lateral margin with two considerable emarginations, with small, hardly perceptible dust-like setae. Posterior margins with apically slightly dilated setae.

Scutellum, small, triangular. Elytra moderately elongate (length-to-width ratio 1:0.705), with ten striae and ten costate intervals. Even elytral intervals (including tenth interval) lower than odd ones, however, still rather costate, their surface considerably more elevated than and thus distinctly differentiated from surface between punctures in striae. Odd intervals with small, dust-like setae, even intervals glabrous. Tibiae slim, anterior tibia with three distinct teeth. Tarsi slim, tarsites only slightly widened apically, upper terminal spur moderately shorter than first metatarsite, lower terminal spur shorter by about 1/2.

Ventral surface dark brown, alutaceous. Metasternal plate moderately impressed medially, with narrow, anteriorly considerably shortened furrow. Abdominal sternites with transverse rows of setae. Pygidium with four setae. Anterior femur wide, with two rows of setae (along posterior margin and behind anterior margin). Intermediate and posterior femora with thin, long setae along posterior margin, shorter setae along anterior margin and three rows of small, semidecumbent setae on ventral surface, each trochanter with thin, long, hairlike seta.

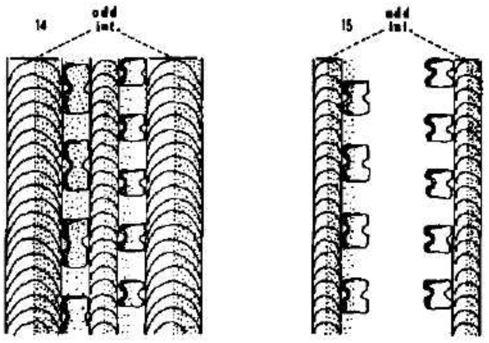
TYPE MATERIAL. Holotype: Sarawak, Kapit dist., Sebong, Balch riv, 9.-21.3.1994, Sv. Bílý leg – in SBCP; paratype 1: the same data – in MRCD; paratype 2: Sarawak, Belaga distr., Long Linau, 19.3.1990, A. Riedel lgt. – RCCP; paratype 3: Indonesia/Kalimantan W., Nanga Sarawal env., Tontang, 24.7.-2.8., J. Schneider lgt., 1993 – in MRCD.

DIFFERENTIAL DIAGNOSIS. *O.* (*P.*) *sarawakensis* sp. n. can be differentiated from related species (*O.* (*P.*) *pittinoi*, *O.* (*P.*) *balthasari*, *O.* (*P.*) *bacchusi* and *O.* (*P.*) *thailandicus* sp. n.) by the following combination of characters: head with a V-shaped swelling, considerable anterior emargination of the pronotum lateral margin and even elytral intervals costate (not flat).

***Odochilus* (*Parodochilus*) *thailandicus* sp. n.**
(Figs 9, 15)

Small (2.7 to 3.0 mm), oblong oval, moderately broader behind, not quite matte, brown (Fig. 9). Head anteriorly granulate, posteriorly with V-shaped swelling and pair of oblique ridges; oblique ridges extended up to swellings above eyes. Genae large, well visible from above.

Pronotum transversal, length-to-width ratio 1:1.459, with four transverse ridges; first to third ridges sharp, continuous, fourth ridge broken into longitudinal keels. Transverse or longitudianl wrinkles in furrows between ridges. Lateral margin with two considerable emarginations, with small, dust-like setae. Posterior margin with apically slightly dilated setae (Fig. 9).



Figs 14–15. Schematic drawing of structure of elytral intervals in two *Odochilus* (*Parodochilus* sbg. n.) species. 14 – *O.* (*P.*) *sarawakensis* sp. n.; 15 – *O.* (*P.*) *thailandicus* sp. n. Abbreviation in figures: odd int. = odd elytral intervals.

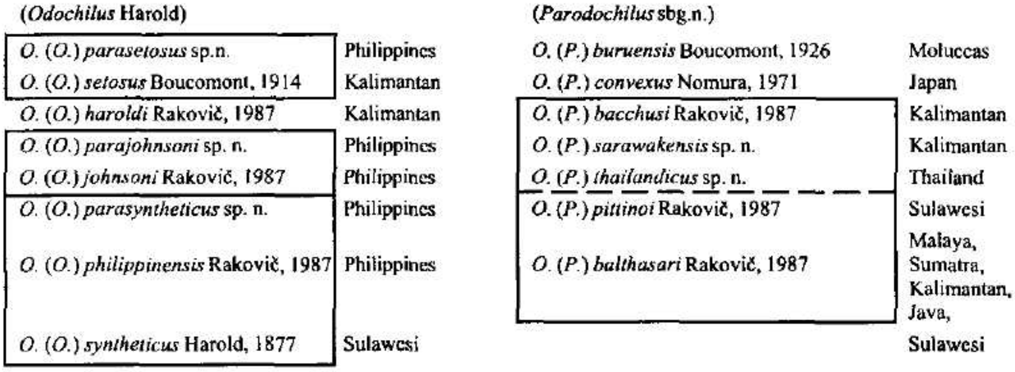

(*Odochilus* Harold)
O. (*O.*) *parasetosus* sp.n.
Philippines
O. (*O.*) *setosus* Boucomont, 1914
Kalimantan
O. (*O.*) *haroldi* Rakovič, 1987
Kalimantan
O. (*O.*) *parajohnsoni* sp. n.
Philippines
O. (*O.*) *johnsoni* Rakovič, 1987
Philippines
O. (*O.*) *parasyntheticus* sp. n.
Philippines
O. (*O.*) *philippinensis* Rakovič, 1987
Philippines
O. (*O.*) *syntheticus* Harold, 1877
Sulawesi
(*Parodochilus* sbg.n.)
O. (*P.*) *buruensis* Boucomont, 1926
Moluccas
O. (*P.*) *convexus* Nomura, 1971
Japan
O. (*P.*) *bacchusi* Rakovič, 1987
Kalimantan
O. (*P.*) *sarawakensis* sp. n.
Kalimantan
O. (*P.*) *thailandicus* sp. n.
Thailand
O. (*P.*) *pittinoi* Rakovič, 1987
Sulawesi
O. (*P.*) *balthasari* Rakovič, 1987
Malaya,
Sumatra,
Kalimantan,
Java,
Sulawesi

Fig. 16. Relationships between particular *Odochilus* Harold species – closely allied species shown in the boxes.

Scutellum small, triangular. Elytra moderately elongate, length-to-width ratio 1:0.670, with ten striae and ten intervals. Odd intervals high, strongly costate, even intervals quite flat, surface of even intervals not differentiated from surface areas between punctures in striae, odd intervals with short, dust-like setae, even intervals glabrous.

Tibiae slim, protibia with three distinct teeth, upper terminal spur of metatibia moderately shorter than first metatarsite, lower spur by about one half shorter. Tarsites subcylindrical, only slightly widened apically.

Ventral surface finely alutaceous, dark brown. Metasternal plate with few very small setae, with narrow, anteriorly strongly shortened furrow (essentially present only in posterior half). Pygidium with four setae, fifth and sixth sternite each with transverse row of distinct setae, fourth sternite with rather indistinct row of setae, remaining sternites glabrous. Anterior femur wide, with small setae along anterior margin. Intermediate and posterior femora with three rows of short setae (along anterior and posterior margins and on ventral surface), each trochanter with long, thin, hairlike seta.

TYPE MATERIAL. Holotype: Thailand, 1.–12.3.1996, Chumphon Prov., Pha To env., 9°48 N 98°47 E, lgt. P. Prudek – ABCB; paratype *1* to *8*: the same data – in *ABCB*; paratypes *9* to *12*: the same data – in *MRCD*.

DIFFERENTIAL DIAGNOSIS. *O.* (*P.*) *thailandicus* sp. n. is distinctively different from any other species of the genus because of having flat even elytral intervals, which are differentiated neither by their elevation nor by their structure from the area between punctures in elytral striae (Fig. 15).

Odochilus (*Parodochilus*) *balthasari* Rakovič, 1987

In the Balthasar's collection, kept in the National Museum in Praha, the author found a specimen of the *O. balthasari* from the Malay peninsula labeled as follows: Malaisie, Johor, Sediti Kechil, Kota Tinggi, 10.–13. VI. 69, R. Pilet.

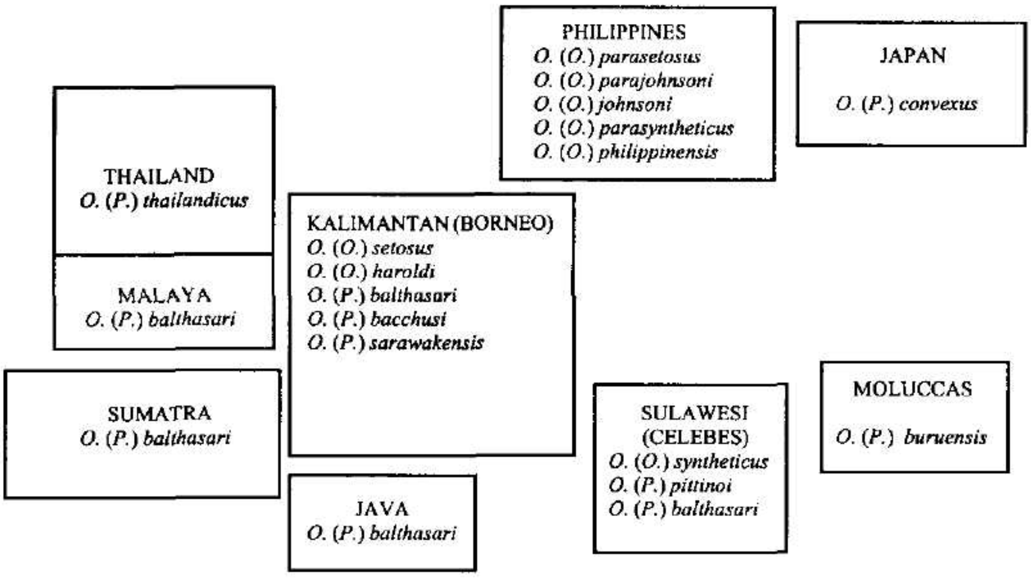


Fig. 17. Distribution of species of the genus *Odochilus* Harold.

Key to species of the subgenus *Parodochilus* sbg. n.

1 (2) Pronotal ridges in form of extraordinarily high lamellae (Fig. 10). 3.4 mm. The Moluccas. .... *O.* (*P.*) *buruensis* Boucomont
2 (1) Pronotal ridges typically strongly convex, with distinct upper edge, however, not in form of high lamellae.
3 (4) Third pronotal ridge broadly interrupted medially, two longitudinal ridges extended backwards from this interruption. 2.6 mm. Japan (Iriomoto Is.). .... *O.* (*P.*) *convexus* Nomura
4 (3) Third pronotal ridge either quite continuous or only narrowly interrupted medially, no longitudinal ridges attached to it.
5 (8) Head vertex with two pairs of oblique ridges.
6 (7) Second pronotal ridge slightly interrupted medially. Posterior oblique ridges on head vertex weak, vestigial (Fig. 13). 3.0 to 3.4 mm. Sulawesi. .... *O.* (*P.*) *pittinoi* Rakovič
7 (6) Second pronotal ridge continuous. Posterior oblique ridges on head vertex well developed, about as long and as high as anterior ridges (Fig. 12). 2.9 to 3.6 mm. Malay Penin., Sumatra with adjacent isles, Java, Kalimantan. .... *O.* (*P.*) *balthasari* Rakovič
8 (5) Anterior pair of oblique ridges on head vertex replaced by continuous, V-shaped swelling.
9 (10) Anterior emargination of pronotum lateral margin either very shallow or quite lacking (Fig. 11), 2.3 to 3.2 mm. Kalimantan. .... *A.* (*P.*) *bacchusi* Rakovič
10 (9) Anterior emargination deep, very distinct.
11 (12) Even elytral intervals lower than odd ones, however, still rather costate, their surface considerably elevated above surface between puntures of elytral striae (Fig. 14). Larger species, 3.1 to 3.3 mm. Kalimantan (Sarawak). .... *O.* (*P.*) *sarawakensis* sp. n.
12 (11) Even elytral intervals quite flat, their surface not differentiated from surface between puntures of elytral striae (Fig. 15). Smaller species, 2.7 to 3.0 mm. Thailand. .... *O.* (*P.*) *thailandicus* sp. n.

DISCUSSION

The genus *Odochilus* currently includes 15 species. Out of them the species *O.* (*O.*) *haroldi*, *O.* (*P.*) *buruensis* and *O.* (*P.*) *convexus* exert outstanding specific characters making easy their differentiation from the other species. Otherwise, we can note the presence of four groups (pairs and threes) of closely related sympatric and/or allopatric species (Fig. 16).

The distribution of particular species is considered here only based on the specimens studied by the present author and, of course, on considering original data on the well documented species *O.* (*O.*) *convexus* (Japan). The numbers of 73 specimens and 33 specimens studies formerly (Rakovič 1987) and currently, respectively, are sufficiently representative with respect to the probably rare abundance of particular species. In the literature, the occurrence of the *O.* (*O.*) *syntheticus* in Australia is quoted, as mentioned by Schmidt (1922). The present author does not know, what specimen(s) is this information based on. He has never seen any specimen of *Odochilus* from Australia. Of course, future studies can bring new data on the occurrence of this genus in Australia and possibly also in New Guinea, however, at the time of the Schmidt s work on his monograph, the *O.* (*O.*) *syntheticus* was the only one described species of the genus and even much later, different species were misinterpreted as *O.* (*O.*) *syntheticus* by several authors. Thus, it is highly improbable that specimen(s) from Australia formerly possibly studied could be just conspecific with the lectotype of the *O.* (*O.*) *syntheticus*. Based on the present knowledge, the distribution of the genus is reliably demonstrated in Thailand, Malaya, the Greater Sunda islands (Sumatra, Java, Kalimantan, Sulawesi and adjacent islands), the Moluccas, the Philippines and Japan (Fig. 17).

In accordance with the present consideration, the *O.* (*O.*) *johnsoni* and *O.* (*O.*) *philippinensis* were also identified by Stebnicka (1993) in material from the island of Leyte (the Philippines), from areas characterized as cultivated land and secondary forest.

It is unfortunately impossible to add any new information to the short notice concerning biology of the genus (Rakovič 1987), since the specimens studied in the present work are not equipped with data, which could be helpful in this respect. Most of them have probably been captured at light.

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BOOK REVIEW

SCHMID G. H., RADUNZ A. & GRÖSCHEL-STEWART U.: **Immunologie und ihre Anwendung in der Biologie.** Stuttgart-New York: Georg Thieme Verlag, 1993. 247 pp. Format 190×120 mm. Softcover, price DM 39.–. ISBN 3–13–771501–6

The authors are specialists in zoology and cell biology affiliated with University and Institute of Technology in Bielefeld and Darmstadt (Germany). Unlike numerous medically oriented textbooks on immunology dealing with clinical problems, the authors directed their attention at general biological aspects of immunology. They open here the less known views on immunochemical methods in the field of biological membranes. This volume is well-illustrated by 97 figures composed of 140 partly three dimensional or two-coloured schemes, and photographs. Featured here are diverse cells of the immune system and their functions, IgM molecules, various curves, cellular structures, functions of biological membranes, schemes of antibody reactions, and chromatographic methods. In 10 tables presented are reviews of chromosome localization in the immune system genes, the origin and functions of cytokines, components of electrone transport in photosynthesis, polypeptides of the thylakoid membrane, the composition of the lamellar system, and other biological phenomena. The volume consists of five chapters supplied with a list of references to the primary literature.

Chapter one presents a theoretical introduction. Outlined there are: a short history of immunology, cells and tissues of the immune system, biologically relevant molecules, receptors, immunoglobulins, variability of antibodies, the complement system, cytokines, and the humoral response. Moreover, emphasized are: properties of antigens, heterogeneity and phylogenic distance of antigens, molecular weight and compatibility, antigen determinants, antibody formation, regulation and evolution of the immune response and other basic terms.

Chapter two is devoted to antibodies as specific probes for detection of molecular and various cellular components, and for the analysis of biological membranes by immunological methods.

Chapter three covers antibodies to proteins and low molecular compounds. Described here are principles of preparation of antibodies to antigens with differentiated immunogenicity, to polysaccharides, glycoproteins, proteins, peptides and nucleic acids, and antigenic substances from various biological substrates. Described here are preparations of monospecific antisera to ferredoxin-NADP$^+$-reductase and chloroplast lipids, to the phytohormones and herbicides.

Chapter four incorporates methodical applications of antibodies while examining their structure and measurement, and various antibody reactions : direct and indirect agglutinations, quantitation of antibodies on biological membranes, diffusion-in-gel, immunoblotting, enzyme immunoassays, immunoelectrophoretic and other procedures.

Chapter five provides insights into the influence of antibodies on membrane functions. There is an exemple of the thylakoid – a membrane element of chloroplast lamellate structure acting in light reactions of photosynthesis. Using immunological methods there is possible to study the relation between membrane structure and function, and the suppression of electrone transport in photosynthesis using antibodies. Antibodies may be prepared also from membrane polypeptides, lipids or pigments. In conclusion, there is a glossary of basic immunological terms.

This book is primarily devoted to biologists giving them a reviewing information on general aspects of the immune system and detailed prescriptions for experiments in the field of immunology. However, it offers also to medical immunologists many interesting and less usual informative insights and original instructive schemes.

Jindřich Jíra

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Topogenesis of visceral organs related to the longitudinal growth of the embryonal axis

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Abstract. Topogenetic shifts of visceral organs relative to the developing spine and segments in chick embryo were studied. It was found, that the developing spine and segments shift relative to the visceral organs: in the cranial part of the embryonic body cranially, in the caudal part of the embryonic body caudally. The stable area, level with the segments 22–23 was found. The more distant from the stable area, the longer the shift observed. The maximal shift, of about 8–12 segments in length was seen after markings level with the first two or three cervical segments. This shift, indicating in reality the intensive growth of the spine and segments, is responsible for the appearance of the neck. The traditionally used terms like the „descensus cordis" and the „descent" of the thyroid gland according our marking experiments are misinterpretations: in reality the neck and head are ascending from these organs.

Growth, topogenesis, chick embryo, marking, heart

INTRODUCTION

The external shape of the embryo, during the process of development, undergoes far-reaching changes: elongation, separation from the extraembryonic structures, development of the appendages. Furthermore, the embryonic body is subdividing into essential parts – head, trunk and tail (for review see e. g. Balinski 1965, Romanoff 1960, etc.). In addition, in higher vertebrates a new body region appears – the neck.

In the same time the developing visceral organs increase in size. Their growth, differential and in particular cases very intensive, interfere with the relative lack of space in the embryonic body. As a result the visceral organs undergo morphological changes and displacements.

The description, implying the mechanism of the displacement of developing organs in mutual space relations, or in relations to the embryonic axis, do not always reflect the real mechanism of the displacement. Terms, like „descensus cordis" (Baer 1828) or the „descent" of thyroid gland (Kölliker 1879) were introduced and are generally used in textbooks and embryologic monographs (e. g. Patten & Carlson 1974, Romanoff 1960, Starck 1965, etc.)

Studies, concerning the neck development in the chick embryo (Künzel et al. 1986, Seichert & Knospe 1987, 1992) revealed the cranially oriented shift of the developing spine and segments, in relation to the visceral organs, in the cranial part of embryonic body. The shift was considered responsible for the thyroid gland displacement during its development (Knospe et al. 1991) and the same was suggested for the heart displacement (Seichert & Knospe 1987, 1992).

However, the heart and the liver do not change their spatial relations throughout the whole embryonic development. In the same time, the liver develops approximatelly in the centre of embryonic body and keeps the central position throughout the whole development.

This implies, that contrary to the cranially oriented shift of the developing spine and segments, in the relation to the visceral organs in the cranial part of the embryonic body, there might exist the opposite shift in the caudal part of the embryonic body. The aim of the present study is to test this assumption.

MATERIAL AND METHODS

Chick embryos, ranging from embryonic day (c. d.) 3.5 to 4 were marked, using a method permitting the formation of lines of india ink particles in living embryonic tissues (Seichert 1965, 1988).

The marks were introduced dorsoventrally in the range between the median and the paramedian plane (stipled strip in Fig. 1B indicates the range of the localisation of the marks) on different cephalocaudal levels of the embryo. The axial structures (spinal cord and notochord) and/or segments and topographically related mesenchyme and visceral organs (see A in Fig. 1) were marked by the continuous stright line.

The marked specimens were sampled immediately after the marking as controles, or after two or three days of further incubation. The samples were treated as follows:

– Fixed in 4% formaldehyde and microdissected. Very small particles of the india ink dispersed within the embryonic tissues were studied with great accuracy under the stereomicroscope, using magnifications ranging from 10× to 50×.

– Fixed in 75% ethanol and stained for the cartilage by modified method of Lundval (1927), to gain more accurate information of the location of marks, with respect to the skeletal primordia.

The deformation of the originally straight lines of marks and the range of the dispersion of particles of India ink enabled the interpretation of the shifts of visceral organs.

Results were documented by Abbe's drawing device, or by photography. In repeated experiments the traced shifts were plotted against semidiagrammatic reconstructions of lateral projections of outlines of axial structures and visceral organs of the embryo (in Fig. 6 each mark represents a summary of findings from 4 to 19 embryos).

The range of displacements were measured aproximatelly and were expressed in the craniocaudal dimension of related segments. The length unite equals the craniocaudal dimension of one segment on the particular level of the embryonic axis (see the length of line Z in table 1 and in Fig. 6).

RESULTS

1. The dorsal part of the marks (localized in axial structures and in segments), that was linear, was not substantially changed by the further growth of the embryo (Fig. 2 and 6). The shifts of the superficial ectoderm, and eventual small shifts between the medullary cord, notochord and differentiating sclerotome, were not the subject of the present study.
2. The linear course of marks was abruptly changed ventrally from the differentiating vertebral bodies. The tiny line of loosselly scatered mark particles (see Fig. 3–6) continued either caudally or cranially.

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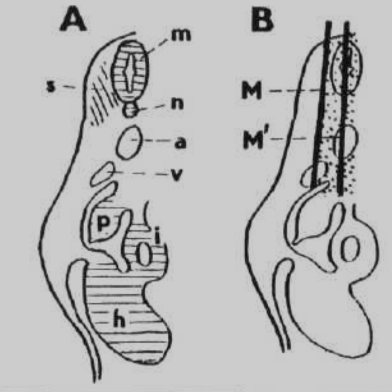
Figs 1–5. 1 – diagram of the transversal section of the chick embryo at the 4th c. d., indicating the essential structures (A), and the approximative marked area (stippled strip in B). M – the mark introduced in the median plane, M – the mark introduced in the extreme paramedian plane, a – aorta, v – cardinal vein, h – hepar, i – intestine, n – notochord, p – pulmo, s – segment m – spinal cord, n – notochord. 2 – the embryo marked at the 4th c. d. and sampled two days later. The mark, introduced cranially to the first segment (the mark labeled Co in the table) did not chage essentially its linear course. 3 – deformation of three marks, introduced at the 4th c. d. level with the segmet 13 (a), 19 (b) and 25 (c). The marked embryos were sampled two days later and photographed after the treatment visualizing the cartillage. Lines of the marks a and b bend caudalwards, contrary to the cranialward bended line of the mark c. 4 – deformation of the mark introduced at the 4th c. d. level with the first segment. Descending part of the mark line reaches the lengths of the craniocaudal dimension of obout twelve segments. The fate of the ventral part of the mark was described in Knospe & Seichert (1991). 5 – the similarly treated embryo as the embryo shown in the Fig. 3. The marks were introduced level with the segments 9/10, 12/13 and 19/20 respectivelly. Length of the bended parts of mark lines are decreasing craniocaudally, so that the line of the caudal mark is nearly stright (arrow).

1



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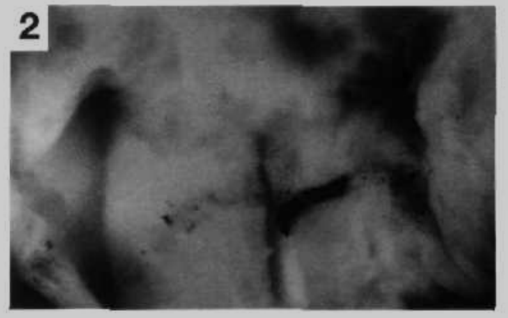

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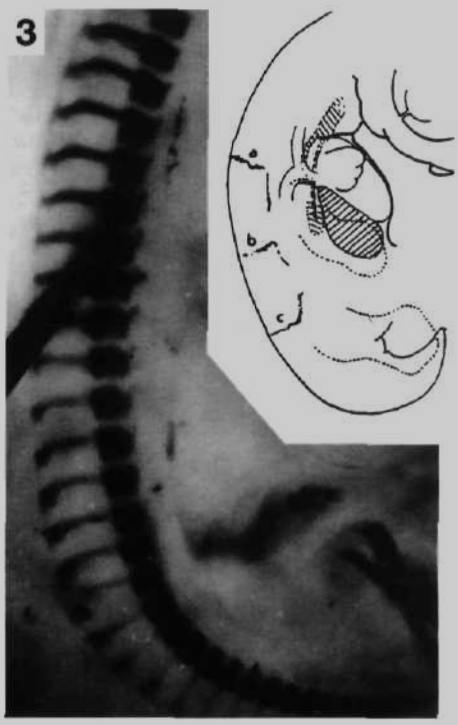

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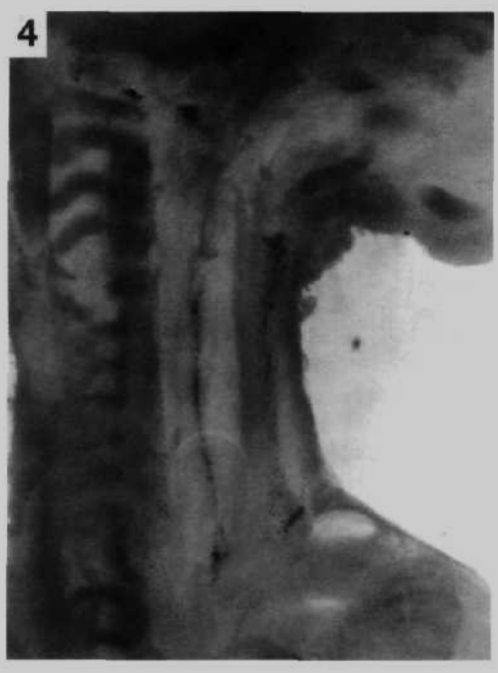

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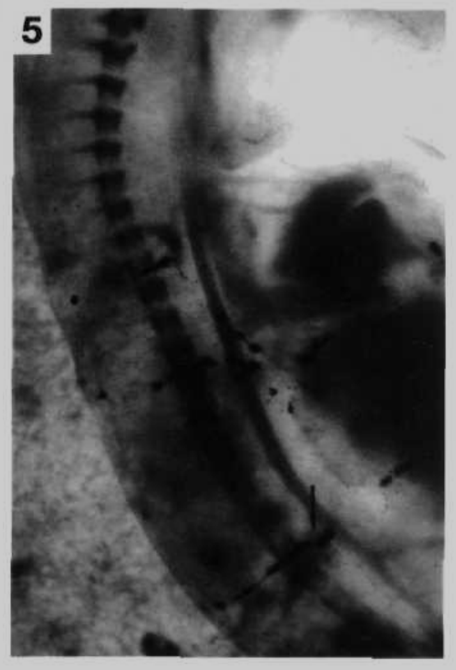

The bending occured in the majority of experiments. The exceptions are presented under heading 3, 4 and 5, and in Fig. 2 and 6.

– The line Z was located in the epibranchial mesoderm, in the most cranial, supracoelomic part of the embryonic body (Fig. 4 and 6). In the part of the embryonic body neighbouring the coelom, the line Z was located in the loose mesenchyme ventrally to the differentiating vertebral bodies, surrounding the dorsal aorta (Fig. 3 and 6). The same picture was seen in the caudal part of the embryonic body.

– The orientation of the line Z depended on the craniocaudal level of the introduction of the mark: the line was bent caudalwards in the cranial part of the embryonic body, and cranialwards in the caudal part of the embryonic body (Fig. 3–6).

6

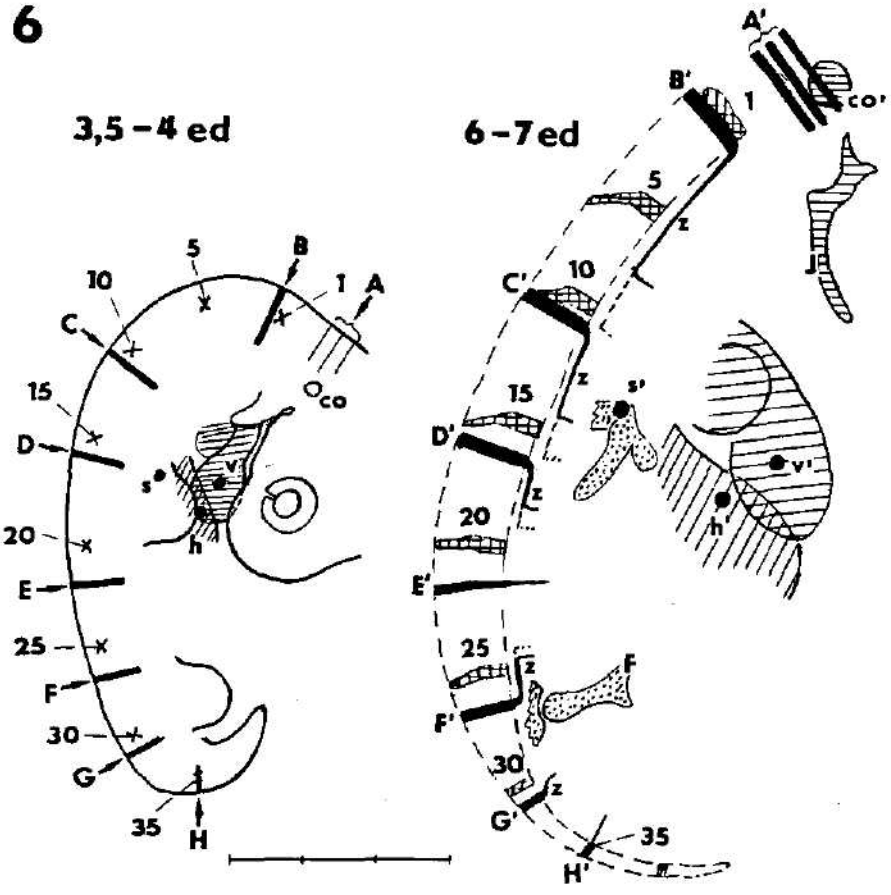

Fig. 6. Schematic lateral projections of the essential parts and organs of chick embryos at the onset (left) and at the end (right) of the experiments. Location of the originally stright lines of marks is indicated in the left part of the figure (A–H) and the deformation of marks after further incubation is shown in the right part (A–H). The line Z indicates both the averrage shift (the continuous part) and the maximal shift (the interrupted part) of axial structures relative to the ventrally located organs. Numbers indicate the number of segments, or the number of the corresponding vertebral anlage. co – capsula otica, h – hepar, j – mandible, s – shoulder, v – heart.

Table 1. *Summarization of measurements of lengths of line Z.* Marking – the embryonic day of mark introduction. Level – number of the segment, indicating the level of the mark introduction. Sampled – embryonic day of sampling. Line Z – lenghts of the line Z expressed in the craniocaudal diameter of neighbouring segments (the unit equals the craniocaudal diameter of one segment on the particular level of the embryomic axis. Symbols indicate the orientation of lines Z, from the point of their abrupt bending: + the line bends caudalwards, – the line bends cranialwards. Co – marks introduced cranially from the first visible segment (up to the capsula otica) – no line Z observed

Marking	Level	Number of embryos	Sampled	Line Z (range)	Line Z (awerage)
3.5–4.5ed	Co	7	6–7ed	0	0
3.5–4ed	1–3	12	6–7ed	8–12 +	8.90 +
3.5–4ed	9–13	16	6–7ed	4–7 +	4.45 +
3.5–4ed	15–17	19	6–7ed	1–3 +	2.40 +
3.5–4ed	22–23	10	6–7ed	0.25 + 1.00 –	0.27 –
3.5–4ed	26–28	14	6–7ed	1–3.5 –	2.06 –
3.5–4ed	30–32	5	6–7ed	0–1.5 –	0.40 –
3.5–4ed	34–36	4	6–7ed	0	0

– The length of the line Z depended on the craniocaudal localisation of the mark (see line Z in table 1 and Fig. 6): the more cranial was the origin of the line Z as to the segment 22, the longer the line was. Caudally from the segment 23, the situation was quite opposite: line Z was oriented cranialwards and its length increased towards the caudal part of the embryonic body (up to the segment 26–28, see the table, Fig. 6 and the § 4).

The measurements of length of the line Z is summarized in the table 1.

3. The line Z did not develop in marks introduced cranially to the first segment (Fig. 2 and A in Fig. 6 and level Co in the table). In such experiments the irregular dispersions of the mark line developed instead of the line Z.

4. None, or neglectable shifts of the developing spine and segments, relative to visceral organs were observed on the level of segments 22 to 23 (see table 1, mark b in Fig. 3, the caudal mark in Fig. 5 and Fig. 6).

5. No shifts were seen from the level of segment 34 caudally (Fig. 6 and Table 1).

6. At the end of the line Z, the mark line bent ventrally and marked visceral organs. The fate of the ventral part of the mark (Fig. 4) was described in Seichert & Knospe (1992), Knospe & Seichert (1991).

DISCUSSION

The line of scattered mark particles (line Z) indicates the shift of the developing spine in relation to the ventrally located organs. The direction of the shift and the interpretation of the developing organ displacements are to be discussed.

Each segment grows in its specific rate (for details see Williams 1910, and review in Romanoff 1960) and the sum of the unequal craniocaudal increase in size of all segments is responsible for the elongation of the embryonic body. There are two observations indicating, according to our opinion, the existence of an active part of the body responsible for the embryonic organs displacements and determining the direction of their displacements:

At first, both the existence of the relative stable area (on the level of somites 21–23) and the orientation and length of the line Z play the crucial role in the interpretation of the true orientation of displacement: Cranially to the stable area, the line Z was oriented caudalwards. Caudally to the stable area, was the line Z oriented cranialwards. The opposite orientation of the line Z as to the stable area indicates active role of the axial structures and segments in the longitunal growth of the embryo. The length of the line Z, which is dependent upon the distance of the mark from the stable area, indicates the orientation of displacements.

Second, the idea of the active role of the axial structures in the organ displacement and the passive role of viscera themselves, is indicated even by the close space relation of the heart and liver (and also of the pulmonal anlage) throughout the whole embryonic dvelopment.

Visceral organs, in the cranial part of the embryonic body, therefore, do not in reality descend. If this were the reality, the line Z would have been increasing towards the stable area. Contrary to the above mentioned assumption, the axial structures are carried away from the space related organs by their own growth. According to these facts the „ascensus colli et capitis“ should be the more appropriate term than e. g. „descensus cordis“.

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